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Introduction

The hammerhead sharks, so named because of the unusual lateral expansion of the head, comprise a moderately large family of sharks occurring in tropical and temperate waters throughout the world. They are a rather old group; fossil remains have been found in Eocene deposits from Virginia (Shelton P. Applegate, pers. comm.). The family belongs to the relatively speciose and poorly known suborder Galeoidea, in which are found most of the large and all of the dangerous kinds of sharks. Since the hammerheads are well defined, and, with one exception, adequate study material exists for all the species, they form an ideal taxon for systematic study.

The most recent works of a revisionary nature that have appeared on the hammerheads (Tortonese, 1950, pp. 1–39; Fraser-Brunner, 1950, pp. 213–219) list eleven and ten species, respectively; however, the above authors were unable to examine examples of all the species treated or all the extant types. Consequently, a number of conclusions were reached that now appear to be erroneous. The following

[1] Florida State Museum, University of Florida, Gainesville.

is a comparison of the systematic arrangements of the family Sphyrnidae, as presented by Tortonese and Fraser-Brunner, with a classification as determined from the present study:

Proposed	Tortonese, 1950	Fraser-Brunner, 1950
Subgenus *Eusphyra* Gill, 1861		
1. *Sphyrna blochii* (Cuvier, 1817)	*Eusphyra blochii* (Cuvier 1817)	*Sphyrna blochii* (Cuvier, 1817)
Subgenus *Sphyrna* Rafinesque, 1810		
2. *Sphyrna mokarran* (Rüppell, 1835)	*Sphyrna mokarran* (Rüppell, 1835)	*Sphyrna tudes* (Valenciennes, 1822)
	Sphyrna tudes (Valenciennes, 1822)	*Sphyrna ligo*, new species
3. *Sphyrna zygaena* (Linnaeus, 1758)	*Sphyrna zygaena* (Linnaeus, 1758)	*Sphyrna zygaena* (Linnaeus, 1758)
4. *Sphyrna lewini* (Griffith and Smith, 1834)	*Sphyrna lewini* (Griffith, 1834)	*Sphyrna lewini* (Griffith, 1834)
	Sphyrna oceanica (Garman, 1913)	*Sphyrna oceanica* (Garman, 1913)
	Sphyrna diplana Springer, 1941	
5. *Sphyrna couardi* Cadenat, 1951		
Subgenus *Platysqualus* Swainson, 1839		
6. *Sphyrna tiburo tiburo* (Linnaeus, 1758)	*Sphyrna tiburo* (Linnaeus, 1758)	*Sphyrna tiburo* (Linnaeus, 1758)
Sphyrna tiburo vespertina Springer, 1940	*Sphyrna tiburo* (Linnaeus, 1758)	*Sphyrna tiburo* (Linnaeus, 1758)
7. *Sphyrna media* Springer, 1940	*Sphyrna media* Springer, 1940	*Sphyrna media* Springer, 1940
8. *Sphyrna corona* Springer, 1940	*Sphyrna corona* Springer, 1940	*Sphyrna corona* Springer, 1940
9. *Sphyrna tudes* (Valenciennes, 1822)	*Sphyrna bigelowi* Springer, 1944	*Sphyrna bigelowi* Springer, 1944

Another nominal species, *Sphyrna nana*, which was recently described by Sadowsky (1965), is regarded as a synonym of *S. media*, for reasons discussed elsewhere in this paper.

Adequate study material exists for all of the above species, with the exception of *Sphyrna couardi*. I have not seen an entire specimen of this species, although I have examined a head; however, the morphology of the head and chondrocranium, together with the patterns of the Ampullae of Lorenzini, indicate that *S. couardi* is a valid form.

A number of structures have been studied that have proved to be useful in the delineation of the species of *Sphyrna*. All species can be distinguished on the basis of head shape alone. Head shape ranges from evenly rounded and spadelike (*Sphyrna tiburo tiburo*) to extremely wide and narrow (*Sphyrna blochii*). Some forms have an

indentation on the median anterior margin of the head, while in others this indentation is lacking. The presence or absence of an outer narial and/or inner narial groove and the relative length of the latter help to distinguish even the smallest individuals of a particular species.

The various chondrocrania also are distinctive. Shape of both the anterior and posterior parts of the preorbital process, degree of development of the "wings" on the olfactory cartilage, development of the rostral "wings," shape of the rostral cartilage, presence or absence of accessory rostral cartilages, presence or absence of a rostral fenestra, and shape of the anterior fontanelle all differ from species to species.

The arrangement of the Ampullae of Lorenzini on the ventral surface of the head is relatively constant for each species, with the arrangement of those in the anterior-median area being particularly diagnostic. These ampullae, which are long canals filled with mucus, comprise a highly modified part of the lateral-line system, and it has been suggested that they may be involved in the detection of temperature changes, hydrodynamic pressure changes, tactile stimulation, and/or electric gradients (Young, 1962, p. 172). For brevity, these structures are referred to as mucal pores throughout this paper.

Teeth vary according to species, although in several instances the differences are rather slight. Shape and arrangement of the teeth, as well as the presence or absence of serrations, are distinctive.

There are differences between the species in size and shape of the fins and in the positions of these structures relative to each other. The positions of the fourth and fifth gill slits in relation to the insertion of the pectoral fin and the relative lengths of the gill slits are important. Finally, the various species differ in the presence or absence of a lower precaudal pit and the shape of the upper precaudal pit.

Recent studies by Drs. Victor G. Springer and J. A. F. Garrick (1964) on carcharhinid sharks indicate that the nature and number of the vertebrae can be an extremely useful taxonomic tool, often showing differences not evident from the study of external morphology. Unfortunately, the value of vertebral characters was not recognized while my study was in progress, and consequently only a few counts were made for the species of *Sphyrna*.

Other characters that are probably of taxonomic importance in hammerheads are the morphology of the pelvic claspers and the electrophoretic patterns of the serum proteins. The latter were not studied because of the unavailability of fresh specimens and lack of facilities. Because of the relatively small size and immaturity of the available specimens, claspers of only three species, *Sphyrna tudes*, *S. media*, and *S. tiburo*, were examined.

Another problem encountered was the scarcity of large specimens; however, I know of no taxonomically significant characters, with the exception of the pelvic claspers, that are not evident in the embryos and young. Although it would be desirable to know the full extent of the various morphometric changes occurring during growth, such data probably would not alter the present taxonomic conclusions.

The degree of confidence in the taxonomic conclusions reached in this paper is dependent largely upon the number of specimens available and on the extent of geographic coverage. The decision reached concerning the status of *Sphyrna mokarran*, therefore, does not rest on as firm a basis as for *S. lewini* and *S. zygaena* because far fewer specimens of *mokarran* were seen and the geographic coverage of the last two species was much better. Only one specimen of *Sphyrna tudes* from the Mediterranean was examined, and, as stated previously, *S. couardi* was represented only by a head. In the case of *S. tudes*, however, only one other specimen of this species outside of the western Atlantic area is known by me to be present in collections.

Acknowledgments

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Wayne J. Baldwin, University of California at Los Angeles; the late Miss Margaret H. Storey, Stanford University; Dr. David K. Caldwell, Los Angeles County Museum; Mr. William I. Follett and Mrs. Lillian Dempster, California Academy of Sciences; Dr. Earl S. Herald and Mr. Robert Dempster, Steinhart Aquarium, San Francisco, Calif.; Drs. Arthur D. Welander and Kelshaw Bonham, University of Washington; Dr. John C. Briggs, University of South Florida; Drs. Reeve M. Bailey and Robert Rush Miller, University of Michigan; Mr. Frank Williams, Director, Guinean Trawling Survey, Lagos, Nigeria; Prof. Enrico Tortonese, Museo Civicio de Storia Naturale, Genoa, Italy; Prof. M. Benazzi and Mr. Alberto Lanfranchi, University of Pisa Museum, Pisa, Italy; Dr. Wolfgang Klausewitz, Senckenberg Museum, Frankfurt-on-Main, West Germany; and to the authorities of the British Museum of Natural History. Finally, I would like to express my special appreciation to Mr. Paul Laessle, staff artist of the Department of Zoology, University of Florida; Mrs. Dorothea B. Schultz; and Mr. Craig Phillips, who are responsible for the illustrations and graphs.

Materials and Methods

Specimens examined or recorded are from the following museum collections: Academy of Natural Sciences of Philadelphia (ANSP); British Museum (Natural History) (BMNH); California Academy of Sciences (CAS); Field Museum of Natural History (formerly Chicago Natural History Museum) (FMNH); Museum of Comparative Zoology, Harvard University (MCZ); Museum National d'Histoire Naturelle (Paris) (MNHN); Scripps Institution of Oceanography (SIO); Stanford University (SU); University of California, Los Angeles (UCLA); Florida State Museum, University of Florida (UF); University of Miami, Institute of Marine Science (UMML); University of Pisa (Italy) (UP); University of Michigan, Museum of Zoology (UMMZ); United States National Museum (USNM).

Proportional measurements for all specimens were made according to the methods described by Springer (1964, pp. 562–568). Measurements are expressed in thousandths of total length (TL). Various external morphological characters are illustrated and labelled in figures 1 and 2. While the specimen on which figure 1 is based is not a member of the family Sphyrnidae, most of the characters apply equally to the hammerhead sharks.

Head-pore and chondrocranial terminologies (figs. 2, 3) are adapted from Daniel (1922, p. 59) and Tortonese (1950a, p. 9), respectively.

All radiographs of the chondrocrania were made on type M Kodak Industrial film with a "hard ray" machine (Miller, 1957, pp. 29–40).

Additional proportional measurements, other than those found in the tables, were also taken. These have not been included, however, since they give no information not already expressed by the measurements in the tables.

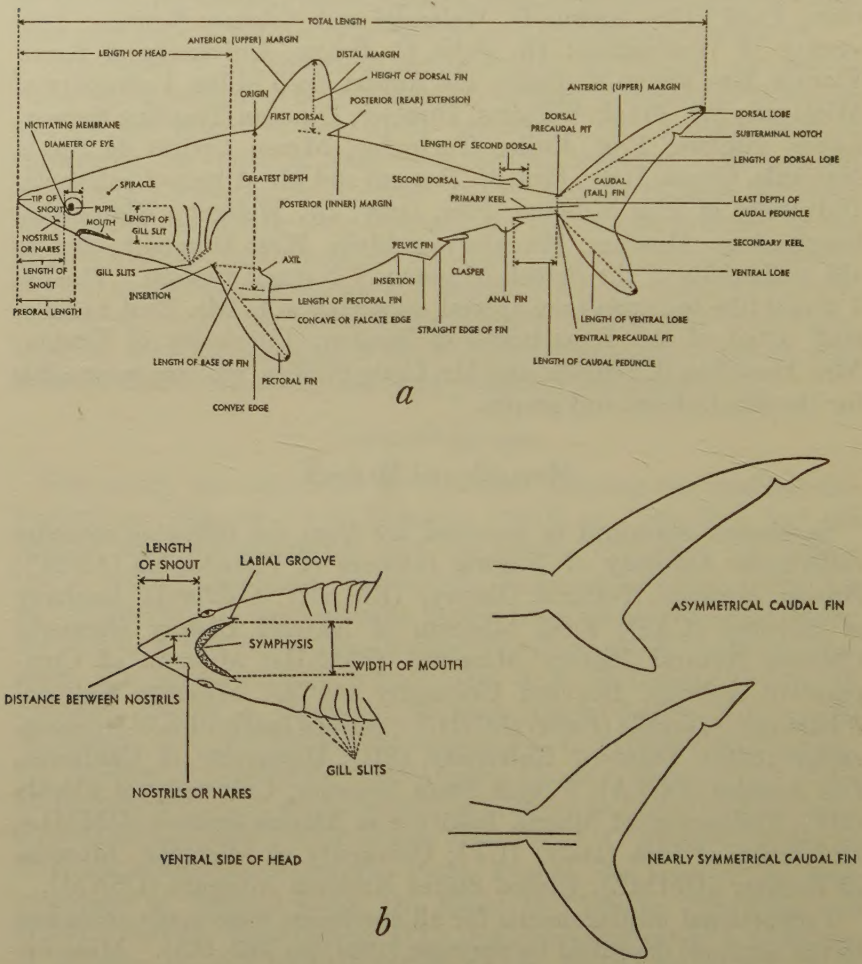


FIGURE 1.—External features of a shark with indications for measurement: *a*, lateral view of body; *b*, ventral view of head and comparison of caudal fins. (Drawings by Craig Phillips, from Garrick and Schultz, 1963, pp. 5, 6.)

As indicated in plates 7C, D, one of the main chondrocranial features separating *Sphyrna corona* and *S. media* is rostral cartilage length. This difference has been expressed as a ratio by dividing the rostral cartilage length by the distance between the tips of the preorbital cartilages (fig. 17). Values were obtained by measuring the distances

between the points marked by X (rostral cartilage length) and Y (distance between tips of preorbital cartilage) in figure 3.

In addition, *S. corona* and *S. media* may also be distinguished by difference in snout length. The values have been expressed as a ratio by dividing snout length by head width; these are compared in figure 16.

In general, determination of the patterns of the Ampullae of Lorenzini on the ventral surface of the head becomes progressively easier with an increase in size of the individual. This is subject to variation, however, even within the same series of specimens.

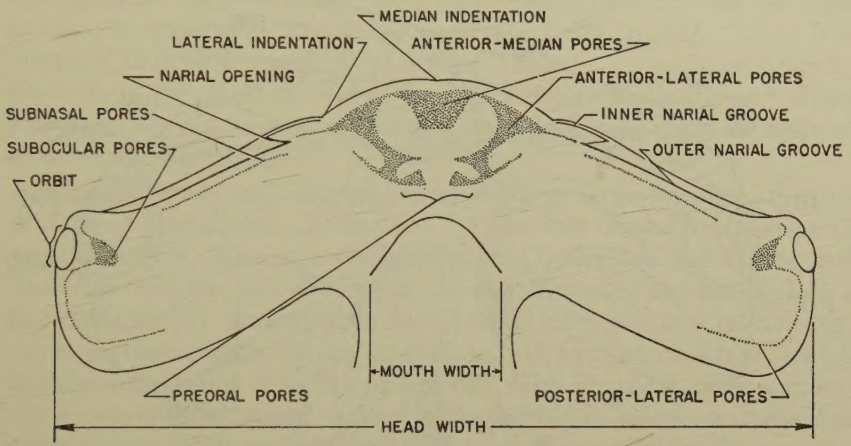


FIGURE 2.—Ventral side of head, showing important morphological features and mucal pore patterns (terminology of mucal pores adapted from Tortonese, 1950a, p. 9; drawing by Paul Laessle).

Since a whole specimen of *Sphyrna couardi* was not available and the head examined was seen after most of the figures were prepared, this species has not been included in the species key, in most of the tables, or in figures 4 and 22. Also, no diagnosis or description is given under the account of the species.

Information regarding life histories, morphometric changes resulting from growth, and zoögeography are usually included in separate sections rather than in the individual species accounts. If, in a species account, there is no discussion of morphological variation, it may be assumed that no noteworthy variation was discovered. New names, new combinations of names, and information pertaining to original descriptions and type material have been included in the synonymies; if the nomenclatural history of a species is of sufficient complexity, additional discussion is presented elsewhere in the species account. More complete synonymies, based on references for the

western Atlantic region, may be found in Bigelow and Schroeder (1948).

Localities from which specimens were examined are represented on the distribution maps by solid symbols; literature records are represented by open symbols.

In the tabulation of proportions values have been separated, as much as practicable, by geographic area. In cases where paucity of specimens does not permit an adequate comparison, and if the specimens do not appear to be different from those from other areas,

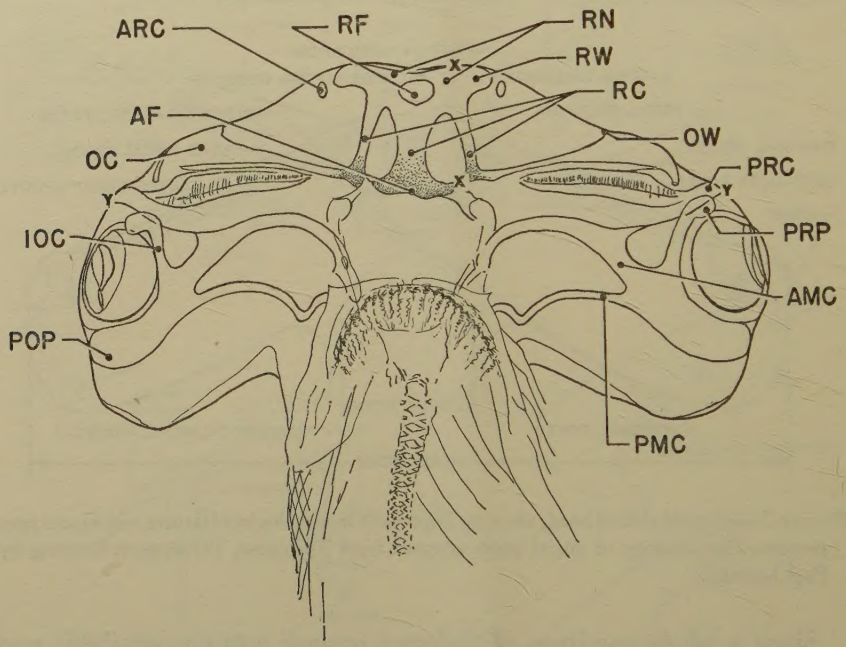


FIGURE 3.—Diagram of hammerhead chondrocranium (terminology adapted from Daniel, 1922, p. 59): AF (anterior fontanelle), AMC (anterior mediorbital connection), ARC (accessory rostral cartilage), IOC (innerorbital cartilage), OC (olfactory cartilage), OW (olfactory wing), PMC (posterior mediorbital connection), POP (postorbital process), PRC (preorbital cartilage), PRP (preorbital process), RC (rostral cartilages), RF (rostral fenestra), RN (rostral node), RW (rostral wing). (Drawing by Paul Laessle).

values have been combined. An exception to this was made in the case of the single specimen of *Sphyrna tudes* from the Mediterranean. This specimen is the holotype, and a comparison with material from the western Atlantic was desirable.

Classification

The hammerhead sharks have, in the past, been accorded family status by most of the investigators responsible for the major works on

fish classification (Gill, 1861, pp. 403–412; Jordan, 1923; Berg, 1940), while others (Regan, 1906, pp. 722–758; Norman, unpubl. ms.) have regarded this group as a subfamily of the Carcharhinidae. Berg's action apparently was based primarily on the studies by White (1937).

Although White (1937) retained the Sphyrnidae as a distinct family, she gave no convincing reasons supporting this decision. Little was said about the relationships of the sphyrnids and carcharhinids, and the only places where they were compared were in the key and in the discussion of the pelvic claspers. While the pelvic claspers obviously constitute a valuable taxonomic character for the separation of various species, their value in determining interspecific relationships has been subject to question. According to White (1937, p. 94), "They [the claspers] tend to vary within the order [Galea] . . . so inconsistently that they are of little value in establishing relationships." Final judgment should be reserved until a more intensive study is made of most or all the species.

The sphyrnids and carcharhinids share a large number of morphological characters. Both have (1) the first dorsal fin anterior to the pelvic fins; (2) no naso-oral groove; (3) the keels of the dermal denticles complete and dentate on the posterior edge and situated on a flat surface; (4) a nictitating membrane; (5) teeth few in number, never multicuspidate; (6) an asterospondylic type of vertebrae, which has the appearance of a "maltese cross" when viewed in cross section; (7) a "scroll type" spiral valve; (8) three rows of valves on the conus arteriosus; and (9) an ovoviviparous type of reproduction.

The fact that the sphyrnids and carcharhinids have so many basic characters in common suggests a close relationship; however, most of these features are found also in other families, some of which are not intimately related to these two groups. The "maltese cross" pattern of the vertebrae is as well developed in the family Triakidae as it is in the carcharhinids and sphyrnids. In addition, the nictitating membrane, which has been thought to be unique to the latter two families, also occurs in the triakids (V. G. Springer and J. A. F. Garrick, in litt.).

Recent unpublished studies by Dr. Shelton P. Applegate indicate that the hammerheads, in addition to the pronounced lateral expansion of the head, differ from carcharhinid sharks in the following ways: (1) The vertebrae, in cross section, show a convexity of the uncalcified canal of the neural and haemal arches that is "butterfly-like" in shape, rather than straight, and (2) in the teeth the lower blade has a smooth, symmetrical arc, whereas in carcharhinid genera there is a definite break in the arc on the side away from the crown. I regard these differences as sufficient justification for continued recognition of the hammerheads as a distinct family.

Genus *Sphyrna* Rafinesque

Cestracion Klein *in* Walbaum, 1792, p. 580. (Type species, *Squalus zygaena* Linnaeus, by subsequent designation of Gill, Ann. Lyceum Nat. Hist. New York, vol 7, p. 403, 1861; name inadmissable, as result of International Commission rulings of 1907 and 1910.)

Sphyrna Rafinesque, 1810, pp. 46, 60. (Type species, *Squalus zygaena* Linnaeus, by subsequent designation of Jordan and Gilbert, U.S. Nat. Mus. Bull. 16, p. 26, 1883.)

Sphyrnias Rafinesque, 1815, p. 93. (Name substituted for *Sphyrna* Rafinesque, 1810.)

Cestrorhinus Blainville, 1816, p. 121. (Type species, *Squalus zygaena* Linnaeus, by subsequent designation of Fowler, Bull. Geol. Surv. New Jersey, vol 4, p. 77, 1911.)

Zygaena Cuvier, 1817, p. 127. (Type species, *Squalus zygaena* Linnaeus, by absolute tautonymy; genus name preoccupied by *Zygaena* Fabricius, 1775, for Lepidoptera.)

Zygoena Risso, 1826, p. 125. (Emended spelling for *Zygaena* Cuvier, 1817.)

Sphyrnichthys Thienemann, 1828, p. 408. (Substituted for *Sphyrna* Rafinesque, 1810.)

Zygana Swainson, 1839, p. 318. (Apparently a typographical error; should be spelled *Zygaena*.)

Platysqualus Swainson, 1839, p. 318. (Type species, *Squalus tiburo* Linnaeus, by original designation.)

Sphyra van der Hoeven, 1855, p. 68. (Emended spelling for *Sphyrna* Rafinesque, 1810.)

Reniceps Gill, 1861, pp. 403, 412. (Type species, *Squalus tiburo* Linnaeus, by original designation.)

Eusphyra Gill, 1861, pp. 403, 412. (Type species, *Zygaena blochii* Cuvier, by original designation.)

Phylogeny.—There has, in the past, been some question as to whether the genus *Sphyrna* has had a monophyletic or polyphyletic origin. Members of the genus are characterized by certain apparently basic morphometric characters, in addition to the widely expanded head, which indicate derivation from a single common ancestor. The most important of these are: No middorsal ridge on the posterior part of the back; dermal denticles not closely overlapping; teeth moderately to strongly oblique; labial furrow either small or absent; body deeply compressed; pectoral fin short. Of the above characters, the last two may have evolved in direct response to the lateral widening of the head, and thus should be viewed with caution. The remaining characters are not likely to have been affected by such a change, and are thus regarded as fundamental evidence of a close relationship among the species of *Sphyrna*. Perhaps the most convincing study supporting a monophyletic derivation has resulted from the work by Starr and Fosberg (1957, pp. 292–295, figs. 1 and 2), in which serum proteins were analyzed using electrophoretic techniques. Work done by various investigators (the most important and extensive being that of C. G. Sibley, of Cornell University, on birds) has shown that the

patterns resulting from these analyses may be valuable indicators of higher relationships in the various groups of vertebrate animals. In the paper by Starr and Fosberg, analyses were made of the serum proteins from one specimen of *Sphyrna lewini*, two specimens of *Sphyrna tiburo*, two of *Rhizoprionodon terraenovae*, and two of *Aprionodon isodon*. The patterns of the latter two species, both of which are members of the family Carcharhinidae, differed notably from each other and from the patterns in the two species of *Sphyrna*. On the other hand, the patterns in *Sphyrna lewini* and *S. tiburo* showed a marked similarity, thus suggesting a close phylogenetic relationship. It would be desirable to run similar tests on *Sphyrna blochii*, which is the most divergent species of hammerhead and the one most likely to have evolved independently. Applegate (in litt.), however, informs me that the teeth in *S. blochii* are similar to those of other hammerheads, although he has not yet studied the vertebrae of this species. In all likelihood, the family Sphyrnidae has had a monophyletic origin.

Sphyrna tudes, *Sphyrna corona*, and *Sphyrna media* show a closer phylogenetic relationship than any other species of hammerheads (fig. 4). All possess a number of common morphological features, some of which are not found in other members of the genus (table 1, figs. 14–22, and pls. 7 C, D and 8). In addition, the three species share several other characters which, although not confined to them alone, further demonstrate a close relationship. The form in which the various characters most closely approach those found in the above species is *S. tiburo* (table 1, figs. 4, 11, 21, and 22, and pls. 7 A, B); as a result, these four apparently closely related species are grouped together in the subgenus *Platysqualus*. The respective lengths of the anal fin and anal fin base, the relative lengths of the gill slits, the diameter of the orbit in relation to the distance from the anterior edge of the orbit to the outer margin of the narial opening, the relative positions of the orbits and anterior part of the mouth, the presence of a lower precaudal pit, the appearance of the upper precaudal pit, and several chondrocranial characters all are similar in these four species. Finally, the species are comparable in size, all apparently reaching a maximum size of about 5 feet.

Within the subgenus *Platysqualus*, *Sphyrna media* seems to show a slightly closer relationship to *S. tiburo* than does *S. corona*. This assumption is based, first, on the greater overall similarity of the chondrocrania (pls. 7 A-D), as well as similarities in appearance of the anterior-median pore patch (figs. 22*e-h*).

The fifth species, *Sphyrna blochii*, is strikingly different from all other species of *Sphyrna* in several characters. The extreme expansion of the head, the presence of an outer narial groove, the greatly decreased total number of vertebrae, and the marked enlargement of the verte-

brae situated over the posterior part of the coelom are all unique to this species, and it is consequently placed in a separate subgenus, *Eusphyra*. *S. blochii* is so different from the other hammerheads that recognition of *Eusphyra* as a genus would not be unwarranted.

Contrary to the relative ease with which the relationships of the preceding species are discerned, those of *Sphyrna zygaena*, *S. lewini*, *S. couardi*, and *S. mokarran* are more difficult. The main feature indicating a fairly close interrelationship among these species is similarity in maximum size. All reach a total length of at least 12 feet, more than twice that attained by any other members of the genus. *S. zygaena* and *S. lewini* (and probably *S. couardi*) have certain features in common, such as a low second dorsal fin with a long lobe; a short anal fin base, the length of which is never more than slightly greater than the pectoral base; a long slender anterior part of the preorbital process of the chondrocranium; a deeply falcate anal fin; and a deep, widely V-shaped upper precaudal pit, with a definite ridge on the anterior margin. This suggests that they probably are more closely related to each other than to *S. mokarran* (fig. 4, table 1, and figs. 6–10).

The following examples, however, illustrate the difficulties one encounters in attempting to determine the relationships of *S. zygaena*, *S. lewini* (including *S. couardi*) and *S. mokarran:* The overall shape of the rostral node, anterior-median pore patch, and anterior part of the preorbital process in the chondrocranium of *Sphyrna zygaena* are most similar to those found in *S. blochii; S. zygaena* and *S. mokarran* are the only hammerheads lacking a wing on the olfactory cartilage; *S. lewini* and *S. mokarran* are the only members of the genus that ordinarily have a rostral fenestra; *S. mokarran* and *S. blochii* have, as do *S. tudes*, *S. media*, *S. corona*, and *S. tiburo*, a rather tall second dorsal fin; *S. mokarran* has, as do *S. tudes*, *S. media*, *S. corona*, and *S. tiburo*, a blunt, clublike knob at the end of the anterior part of the preorbital process of the chondrocranium; and *S. mokarran* is unique, among the hammerheads, in having a deeply falcate pelvic fin.

Despite the difficulties encountered in interpreting the relationships of the above four species, they appear to be related more closely to one another than to any other group of species of *Sphyrna* and thus are included in the subgenus *Sphyrna*.

In the preceding discussion, nothing was said regarding head width, although this is almost the only basis for previous separations of the genus *Sphyrna* into separate genera and subgenera. For example, Tortonese (1950a, pp. 3–6) placed *Sphyrna tiburo* in the subgenus *Platysqualus* and placed *Sphyrna blochii* in a separate genus, *Eusphyra*. Although I have followed both of these allocations (in modified form),

the differences in head width have had comparatively little to do with my decision.

The phylogenetic conclusions may be summarized as follows:

1. The nine species of *Sphyrna*, on the basis of morphological evidence and electrophoretic analyses of serum proteins, likely evolved from a single common ancestor.

2. *Sphyrna tudes*, *Sphyrna corona*, and *Sphyrna media*, with numerous identical morphological characters, some of which are unique, are regarded as the most closely related members of the genus *Sphyrna*.

3. *Sphyrna tiburo*, with a number of morphological characters similar to those in *S. tudes*, *S. corona*, and *S. media*, appears to occupy a phylogenetic position intermediate between these three species and other members of the genus *Sphyrna*. Therefore, because of their close relationship, the four species are placed in the subgenus *Platysqualus*.

4. *Sphyrna blochii* possesses several characters that are markedly different from those found in other hammerheads, such as an extremely expanded head, an outer narial groove, a reduced number of vertebrae, and enlarged vertebrae over the posterior part of the coelom. It is placed in a separate subgenus, *Eusphyra*, although elevation of this taxon to the generic level might be justified.

5. The interrelationships of *Sphyrna zygaena*, *S. lewini*, *S. couardi*, and *S. mokarran* are more difficult to determine, although *zygaena*, *lewini*, and *couardi* seem to show a closer relationship to each other than to *mokarran*. The most important feature shared by the four species is their large maximum size. They are referred to the subgenus *Sphyrna*.

Growth changes.—Certain modifications in shape of the head of sphyrnids occur with increase in size and age, for which there is nothing comparable in other carcharhinid sharks. In young hammerheads, particularly embryos, the anterior margin of the head is more or less broadly rounded, becoming gradually straighter with increase in size and age until sometimes, as in *Sphyrna mokarran* and *Sphyrna tudes*, this margin is nearly straight (figs. 7*a* and 20*c*). In *Sphyrna blochii*, which has the most widely expanded head of any member of the genus, the lateral extensions of the head in embryonic and early postembryonic specimens are nearly parallel to the body axis (fig. 5*c*). With an increase in size of the individual, these structures become situated nearly perpendicular to the body (fig. 5*b*). It has long been thought that such changes in head shape would make hammerhead taxonomy a difficult problem. Such is not the case.

Those head characters of greatest importance in distinguishing species of sphyrnids, such as structure of the chondrocranium, nature of the intranarial and extranarial grooves, and pattern of the mucal

pores on the ventral surface of the head, appear to change very little throughout life, whereas the shape of the fins may be modified with an increase in body size. Other postcephalic features seem to remain fairly constant.

Negative allometric growth occurs in the head of sphyrnids since, with an increase in total body length, there is a proportional decrease in the following characters: Width of head, tip of snout to nares, tip of snout to orbit, tip of snout to symphysis of jaws, diameter of orbit, and intranarial width.

The shape of the upper precaudal pit, changing with an increase in size of the individual, undergoes the greatest modification during

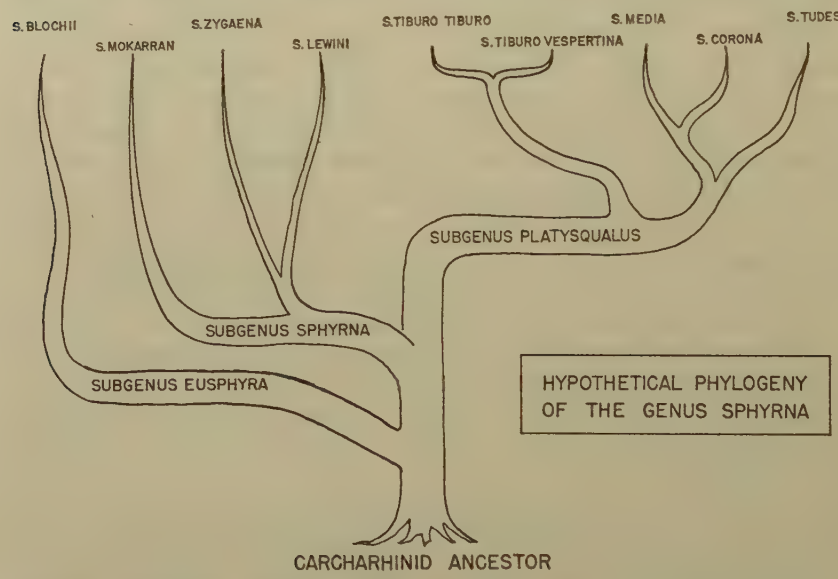


FIGURE 4.—Hypothetical phylogeny of the genus *Sphyrna* (figure by Paul Laessle). (*S. couardi*, which was not included, is closely related to *S. lewini*.)

early growth and likely reaches its final form before the shark is 1,000 mm. long; this is illustrated, from specimens of *Sphyrna media* measuring 356 and 900 mm. TL, in figures 21*f*, *g*.

Other morphometric changes are indicated with an increase in size (tables 2–9), although more large specimens must be examined before the validity of these changes can be established. Pronounced modifications, particularly in length of the trunk between the axil of the pectoral fin and the insertion of the pelvic fin, have been shown to occur in squaloid sharks (Garrick, 1960, pp. 546–548). Since most squaloids do not reach a very large size, however, considerable changes in body proportions can occur with a relatively small increase in total

body length. The galeoid sharks, on the other hand, usually reach a much larger size, and thus proportional changes are not likely to be so pronounced within a comparable size range.

As indicated previously, a straightening of the fins and fin lobes occurs as the shark approaches maturity. In this process the fins (particularly the first dorsal) become increasingly more erect and pointed, whereas the anal fin tends to become somewhat more falcate. In contrast to these true morphometric changes are the unfolding of the fins after birth, a phenomenon that might be compared with the situation in a newly emerged butterfly. Curling of the fins is most pronounced in embryos of *Sphyrna mokarran*, although the reason for this is not clear.

The dermal denticles undergo a noticeable morphological change with an increase in size and age, showing an increased number of "teeth" on the posterior margin. As indicated by Bigelow and Schroeder (1957, p. 24), however, this does not result from changes in the original denticle, but instead occurs as the result of one or more denticle replacements.

In *Sphyrna lewini* there is a progressive darkening of the tips of the pectoral fins with increasing size and age, so that in large specimens these extremities are black. This also may be true to a greater or lesser degree for *S. zygaena* and *S. mokarran*, although I have not yet substantitated it.

Variation among specimens of the same species is discussed under the accounts of the individual species.

Life history and ecology.—No detailed discussion of hammerhead ecology is presented here, since most of the available information has appeared in works by Springer (1939, pp. 9–41; 1940b, pp. 188–194), Bigelow and Schroeder (1948, pp. 407–449), and Baughman and Springer (1950, pp. 96–152). The following is a summary of the information appearing in their papers.

The larger species of *Sphyrna* (*S. zygaena*, *S. mokarran*, *S. lewini*, and, presumably, *S. couardi*) apparently occur both in inshore and offshore waters and have even been known to move into brackish areas. *S. tiburo*, in contrast, seems to prefer shallow embayments and rarely ventures far from land. Little is known about the habitat of the remaining three species.

Hammerheads swim near the surface of the water. It is doubtful if any species descends to very great depths, since there have been no verified captures below a hundred fathoms (Stewart Springer, in litt.).

Sphyrnids feed largely on fish and squid and also may take such items as shrimp, crabs, stingrays, and sharks, including individuals of their own species. The larger hammerheads are regarded as danger-

ous, and there are substantiated records of fatal attacks on humans (Gudger, 1937, pp. 417, 418).

Hammerheads along the eastern North American coast are known to migrate northward in summer and southward in winter, often traveling in schools in both inshore and offshore waters (Bigelow and Schroeder, 1948, pp. 442–444). To the north, *Sphyrna zygaena* is the only species involved in such migrations, whereas, to the south, *S. lewini* is the predominant species. The fact that the only specimens of *Sphyrna zygaena* seen by me from south of the Carolinas (UMML 5639 and UMML 10444, from Miami, Fla.) were taken in winter seems to confirm this. Presumably similar migrations occur in other parts of the world.

Although *S. media* and *S. corona* have been taken in the same areas from Panama Bay north to southern Mexico (map 5), in only one of the collections examined (from Chiapas, Mexico) were the two actually taken together. Whether this is due to a partial ecological separation or simply to lack of material is presently not known.

The number of young in a brood appears to be directly proportional both to size of the individual and to maximum size of the species. The smallest recorded brood (8) was found in *S. tiburo*, the largest (38) in *S. mokarran*.

Zoogeography.—The present distribution of the hammerhead sharks indicates, on the whole, a slow rate of evolution. The members of the subgenus *Sphyrna* (*S. zygaena*, *S. lewini*, *S. couardi*, and *S. mokarran*) apparently have undergone no intraspecific differentiation, despite worldwide distributions (for three of the four species) and long periods of separation of the various segments of their respective populations. The five forms included within the subgenus *Platysqualus* (*S. tudes*, *S. corona*, *S. media*, *S. tiburo tiburo*, and *S. tiburo vespertina*) are morphologically similar to one another, and thus presumably have undergone a more recent evolution. Only in the case of *S. tiburo* is it possible to estimate how long it has taken for evolution to have occurred, because the two subspecies probably differentiated following the most recent (Pliocene) emergence of the Central American isthmus. However, the presence of individuals of this species with a head shape more or less intermediate between typical *tiburo* and *vespertina* indicates that the above explanation may not be as simple as first appears. Possibly the initial separation goes farther back and the intermediate examples have resulted from a partial reamalgamation of the stocks.

Insufficient evidence exists to explain the present distribution of *S. tudes*, *S. corona*, and *S. media*. Evolution of these three species is almost certainly correlated with the various submergences and emergences of the Central American land mass, although it is impossible

to determine the exact sequence of events. Judging from morphological evidence, however, *S. tudes* evolved first, later followed by differentiation of the other two species. The presence of *S. tudes* in both the Mediterranean and western Atlantic is unusual in that few species display such a distribution pattern. This common occurrence may be due either to recent migration in one direction or the other, or to a long period of isolation during which the two populations have, for some reason, failed to differentiate to the species level.

The distribution of *Sphyrna zygaena* is a classic example of an antitropical distribution (Ekman, 1953, p. 250). Presumably the now-disjunct north-south distribution of this species (map 2) was continuous during one or more of the Pleistocene glacial periods, when equatorial waters were cooler than at present. As the glaciers retreated and seas became warmer, *S. zygaena* gradually disappeared from the tropical regions, perhaps remaining for a time in deeper waters where temperatures were cooler (equatorial submergence).

One may conclude from present distributions that the subgenus *Platysqualus* evolved in the western Tethys Sea, a prehistoric body of water that formerly extended from the Eastern Pacific-West Indian region to what is now southeast Asia (Ekman, 1953, pp. 63–67). Should it have evolved in the Indo-Pacific region, one or more species of the subgenus would likely still be found there, since environmental conditions in this area have remained stable over a long period of time. The subgenus *Eusphyra* apparently evolved in the Indo-Pacific, as the only included species, *Sphyrna blochii*, is restricted to that region. It is impossible to determine the center of origin of the subgenus *Sphyrna*, since three of the species in this group have a worldwide distribution.

Key to Species of *Sphyrna*

(Based primarily on specimens 1,000 mm. TL or smaller)

1a. Greatest maximum width of head almost 50 percent of total body length; outer narial groove present; nares not present near eyes, situated more than half distance from eyes to anterior-median notch; upper precaudal pit as in figure 21*a;* anterior-median pores on ventral surface of head as in figure 22*a;* chondrocranium as in plate 5. . . . **Sphyrna blochii** (Cuvier) Indo-Pacific region, from Persian Gulf to northern Australia and southern Philippines.

1b. Greatest maximum width of head not more than 32 percent of total body length; outer narial groove absent; nares present near eyes; upper precaudal pit not as in figure 21*a;* anterior-median pores on ventral surface of head not as in figure 22*a;* chondrocranium not as in plate 5 2

2a. Anal fin and base longer, former measuring from 9.8 to 13.5 percent, and latter from 6.5 to 9.9 percent of total body length; fifth gill slit about as long as first gill slit, both somewhat shorter than three middle slits; fifth gill slit situated above insertion of pectoral fin; orbit smaller, its horizontal diameter less than shortest distance from anterior edge of

orbit to outer margin of narial opening (at least in smaller specimens); teeth relatively weak, median ones often more or less needle-like in appearance; lower precaudal pit present (may also be present in *S. lewini*); posterior lobe of first dorsal fin extending beyond insertion of pelvic fin (in *S. tudes*, *S. corona*, and *S. media* only); maximum size smaller, the largest specimens probably not over 4 or 5 feet TL . . . 3

3a. Head not widely expanded, greatest width about 21 percent of total body length (usually less than 20 percent); anterior margin of head evenly rounded or slightly pointed in median line, never with median notch; posterior lobe of first dorsal fin terminating anterior to insertion of pelvic fin; origin of first dorsal fin situated well posterior to axil of pectoral fin; eyes not situated distinctly anterior to mouth, line drawn between posterior margins of orbits either intersecting or passing just anterior to symphysis of lower jaw; upper precaudal pit as in figure 21*e;* anterior-median pores on ventral surface of head as in figure 22*e;* chondrocranium as in plates 7A, B 4

4a. Head with more evenly rounded anterior margin (fig. 12*b*); greatest width of head measuring slightly less as shown in table 6; fig 13

Sphyrna tiburo tiburo (Linnaeus)

Western Atlantic, from New England to southern Brazil.

4b. Head with less evenly rounded anterior margin (fig. 12*a*), usually coming to a point at tip of rostrum; greatest width of head measuring slightly more as shown in table 6; fig. 13.

Sphyrna tiburo vespertina Springer

Eastern Pacific, from southern California to Equador.

3b. Head widely expanded, the least width 22 percent of total body length; anterior margin of head not always evenly rounded, usually with a more or less distinct median notch (sometimes evenly rounded in *S. media*); posterior lobe of first dorsal fin terminating posterior to insertion of pelvic fin; origin of first dorsal fin situated above or slightly posterior to axil of pectoral fin; eyes situated anterior to mouth, line drawn between posterior margins of orbits passing well anterior to symphysis of lower jaw; upper precaudal pit not as in figure 21*e*; anterior-median pores on ventral surface of head not as in figure 22*e*; chondrocranium not as in plates 7A, B 5

5a. Inner narial groove present; well-defined median notch present on anterior margin of head; anterior-median pores on ventral surface of head as in figure 22*h*; chondrocranium as in plates 8A, B.

Sphyrna tudes (Valenciennes)

Gulf of Mexico south to Uruguay; also recorded from western Mediterranean Sea.

5b. Inner narial groove absent; no well-defined median notch present on anterior margin of head (poorly defined notch may be present in some individuals); anterior-median pores on ventral surface of head not as in figure 22*h*; chondrocranium not as in plates 8A, B . . . 6

6a. Distance from tip of snout to symphysis of upper jaw slightly shorter, usually less than 40 percent of head width (table 7; fig. 16); anal fin more deeply falcate, with a more pointed apex (figs. 14*a*, 15*a*); mouth slightly broader (figs. 14*b*, 15*b*); anterior-median pores on ventral surface of head as in figure 22*f*; chondrocranium as in plate 7C; maximum size possibly larger, the largest specimen

examined about 3½ feet long . . . . . **Sphyrna media** Springer
Eastern Pacific, from Panama to Gulf of California; also in southern Caribbean and southwestern Atlantic, from Panama to Brazil.

6b. Distance from tip of snout to symphysis of upper jaw slightly longer, usually more than 40 percent of head width (table 8; fig. 16); anal fin less deeply falcate, with a more rounded apex (fig. 18*a*); mouth slightly narrower (fig. 18*b*); anterior-median pores on ventral surface of head as in figure 22*g*; chondrocranium as in plate 7D; maximum size possibly smaller, the largest specimen examined a little over 2 feet long . . . **Sphyrna corona** Springer
Eastern Pacific, from Colombia to southern Mexico.

2b. Anal fin and base shorter, former measuring from 8.2 to 10 percent, and latter from 3.8 to 6.7 percent of total body length; fifth gill slit shorter than first gill slit (fourth gill slit about as long as first gill slit); fifth gill slit situated behind insertion of pectoral fin; orbit larger, its horizontal diameter greater than shortest distance from anterior edge of orbit to outer margin of narial opening; teeth broad, not needle-like in appearance; lower precaudal pit absent; posterior lobe of first dorsal fin not extending to above insertion of pelvic fin; maximum size larger, some individuals reaching 20 feet TL 7

7a. Inner narial groove absent; pelvic fin falcate; second dorsal fin higher, length of its anterior margin greater than length of anterior margin of anal fin; lobe of second dorsal fin shorter, not extending nearly to caudal pit, and, when extended vertically upward, about equal to greatest height of fin; teeth strongly serrate, even in small individuals; anterior-median pores on ventral surface of head as in figure 22*b*; chondrocranium as in plate 6A . . . . **Sphyrna mokarran** (Rüppell)
Circumtropical in distribution, but apparently absent from the more isolated oceanic islands.

7b. Inner narial groove present; pelvic fin not falcate; second dorsal fin lower, length of its anterior margin less than length of anterior margin of anal fin; lobe of second dorsal fin longer, extending nearly to caudal pit, and, when extended vertically upward, definitely exceeding greatest height of fin; teeth smooth in small individuals, often weakly serrate in large individuals; anterior-median pores on ventral surface of head not as in figure 22*b*; chondrocranium not as in plate 6A 8

8a. Median notch absent from anterior margin of head; inner narial groove extending at least halfway from narial opening to median part of anterior margin of head; base of anal fin shorter, about equal in length to base of second dorsal fin and slightly less than base of pectoral fin; rostral fenestra ordinarily absent; anterior-median pores on ventral surface of head as in figure 22*c*; chondrocranium as in plate 6C.

Sphyrna zygaena (Linnaeus)
Antitropical in distribution; occurring in cooler waters of northern and southern hemispheres, but absent from intervening tropical waters.

8b. Median notch present on anterior margin of head; inner narial groove not extending halfway from narial opening to median part of anterior margin of head; base of anal fin longer, greater in length than bases

of either second dorsal or pectoral fins; rostral fenestra present; anterior-median pores on ventral surface of head as in figure 22*d*.*
Sphyrna lewini (Griffith and Smith)
Circumtropical in distribution; common in all warm seas.

**Sphyrna couardi* Cadenat keys out to this point, but was not included here since a whole specimen was not examined. It differs from *S. lewini*, however, in having a deeper and more robust head (pl. 9), in minor differences in the chondrocranium (pl. 10), in having the anteriomedian pore patch completely instead of partially divided, and (according to the original description) in having the tips of the pectoral fins white.

Dignaosis of Family and Genus

Distinguished primarily by the shape of the head, which is expanded laterally, and which is accompanied by a corresponding modification of the chondrocranium. Eyes situated at tips of lateral expansions, and nares situated at varying distances along anterior margin of head. Olfactory capsules and orbital region widely expanded, and the three rostal cartilages broadly expanded where joined anteriorly. Midline of back posterior to first dorsal fin without a middorsal ridge. Second dorsal fin always much smaller than first dorsal. Body compressed, the depth of the trunk (measured at origin of first dorsal) from 4 to 5½ times in distance from tip of snout to upper precaudal pit. Caudal peduncle about two-thirds as wide as deep. Upper precaudal pit strongly developed. Lower precaudal pit present in some species, absent in others; when present, not as prominent as upper pit and only about half as wide.

Subgenus *Eusphyra* Gill

The subgenus *Eusphyra*, which includes only *Sphyrna blochii*, is distinguished by the following unique characters: Head extremely expanded, the greatest width from 42.0 to 49.2 percent of total body length; outer narial groove present; total number of vertebrae few (117 and 124 in two specimens examined); body vertebrae 51 to 54, there being from 15 to 16 fewer body than caudal vertebrae; vertebrae over posterior part of coelomic cavity expanded in size; upper precaudal pit merely a narrow longitudinal groove (fig. 21*a*); orbit separated from nares by a distance many times diameter of orbit; a unique anterior-median pore patch on underside of head, the patch characterized by a sharp, pointed angle at outer-posterior corner and a more or less straight posterior edge (fig. 22*a*); and various chondrocranial characters (pl. 5).

Sphyrna (Eusphyra) blochii (Cuvier)

FIGURES 5, 21*a*, 22*a*; PLATES 1, 5

Squalus zygaena (misidentification) Bloch, 1785, vol. 1, pl. 117. (Figure.)
Zygaena blochii Cuvier, 1817, p. 127. (Original description [in footnote]: "Ajoutez l'espèce représentée par Bl. 117, reconnaissable à ses narines placées bien plus près du milieu [*Z. Nob. Blochii*]. Sa deuxième dorsale est

aussi bien plus près de la caudale. L'espèce à large tête, donnée, sous le nom de *pantouflier*." Description based on figure in Bloch, 1785; no type specimen; no type locality.)
Zygaena latycephala van Hasselt, 1823, p. 315. (Originally written *Latycephala;* type locality, Java.
Zygaena laticeps Cantor, 1837, p. 315. (Original description; based on adult specimen of *S. blochi;* type locality, Calcutta.)
Zygana laticeps Swainson, 1838, p. 134. (Illustration of head; generic name misspelling of *Zygaena*.)
Sphyrna blochii Müller and Henle, 1841, p. 54. (Locality unknown.)
Sphyrnias blochii Gray, 1851, p. 50. (India; Singapore.)
Eusphyra blochii Gill, 1861, pp. 403, 412. (Name; new generic name.)
Cestracion (*Zygaena*) *blochii* Duméril, 1865, p. 383. (Indian Ocean.)
Sphyrna zygaena (misidentification) Bridge, 1904, p. 450. (Figure.)
Zygaena blochi Volz, 1907, p. 237. (Benkulen, Sumatra.)
Sphyrna blochi Pellegrin, 1912, p. 2. (Singapore.)
Cestracion blochii Garman, 1913, pp. 156–157. (Synonymy; description; range.)
Cestracion blochi Hora, 1924, p. 464. (Tale Sap, Siam.)
Sphyrna (*Eusphyra*) *blochii* McCulloch and Whitley, 1925, p. 129. (Reference.)

Specimens examined.—(Range in size: 333–880 mm. TL). Pacific Ocean: British North Borneo: SU 13815 (1), no further data; FMNH 21836 (1), Sandakan. Burma: SU 14495 (1), FMNH 40914 (1), Southern Moscos group, South Island. India: SU 41989 (1), Krusadai Island, Gulf of Mannar, Pumbau District, Madras; USNM 195846 (2), ANSP 69397 (1), Bombay. Java: FMNH 15655 (1), FMNH 15656 (1), UMMZ 177111 (6), MCZ 1389 (1 mutilated head), Batavia. Malaya: BMNH 1902.5.28.37 (1), coast of Perak; BMNH 1860.3.19.890 (2), Singapore.

Nomenclature.—Although *Sphyrna blochii*, in common with the other hammerheads, has been placed in several different genera, *Eusphyra* is the only genus which has been erected (Gill, 1861, p. 412) for the sole reception of this species. Gill considered that two unique morphological features of *blochii* (the position of the nares, which are nearer the tip of the rostrum than the eyes, and the extreme elongation of the lateral extensions of the head) constituted sufficient reason for placing the species in a distinct genus. There has been some difference of opinion among recent investigators as to whether *Eusphyra* should be regarded as a good genus. In some of the most important recent works (Bigelow and Schroeder, 1948; Tortonese, 1950a) this classification has been followed, but in an even greater number of cases it has been considered a subgenus of *Sphyrna*. For reasons that are discussed elsewhere in this paper, I follow the latter alternative.

Diagnosis.—See diagnosis of subgenus *Eusphyra*.

Description.—Meristic data appear in table 2. Characters mentioned in the diagnosis of the subgenus *Eusphyra* are not repeated here. A comparison of *S. blochii* with other members of the genus is presented in table 1.

Intranarial distance from one-seventh to one-sixth of TL; anterior margin of head broadly curved medially, the lateral expansions of the head pointing posteriorly in embryonic individuals and extending nearly perpendicularly from body in larger specimens; distinct median scallop present on anterior margin of head; inner narial groove present and distinct, extending about half of distance from narial opening to

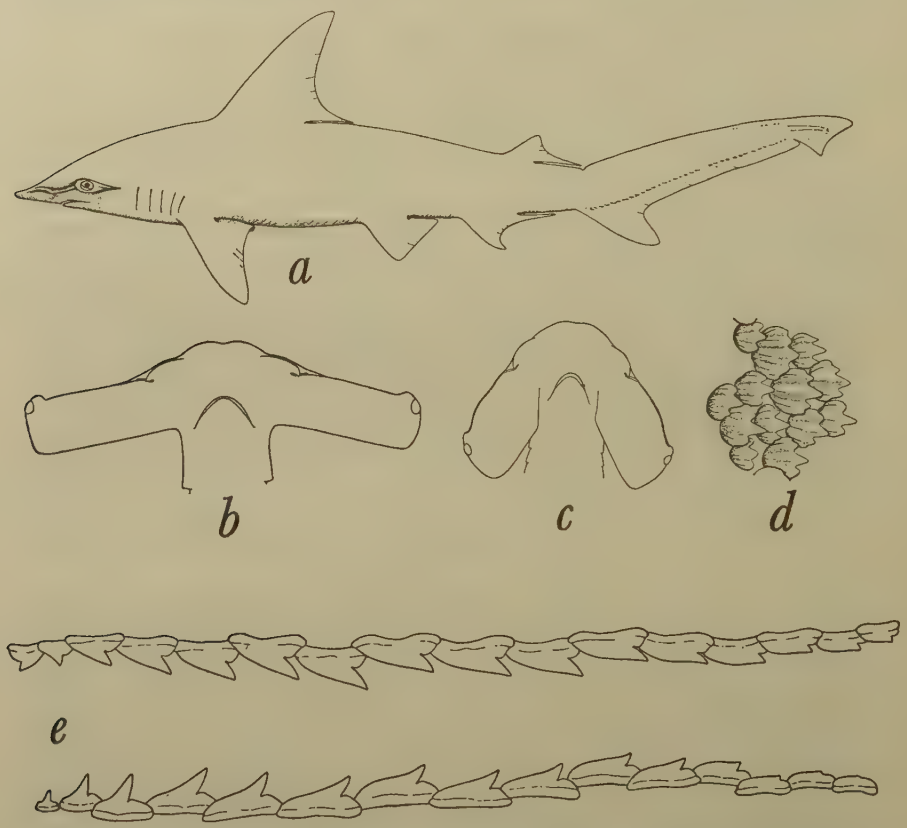


FIGURE 5.—*Sphyrna blochii*: *a*, female, 622 mm. TL, from Sandakan, North Borneo (FMNH 21836); *b*, head of adult, 0.2 × natural size (FMNH 21836); *c*, head of juvenile, 333 mm. TL, from Batavia, Java, 0.6 × natural size (UMMZ 177111) *d*, dermal denticles (FMNH 21836); *e*, teeth series from left side of upper and lower jaws (FMNH 21836). (Drawings by Dorothea B. Schultz.)

median scallop; narial depression present; outer posterior corner of lateral expansions of head situated posterior to corner of mouth in specimens of all sizes; narial flap broad, blunt at tip, with the outer edge curving gradually inward; length of snout about one-eighth of head width; greatest transverse distance between corners of mouth about one-seventh of greatest width of head; symphysis of jaws

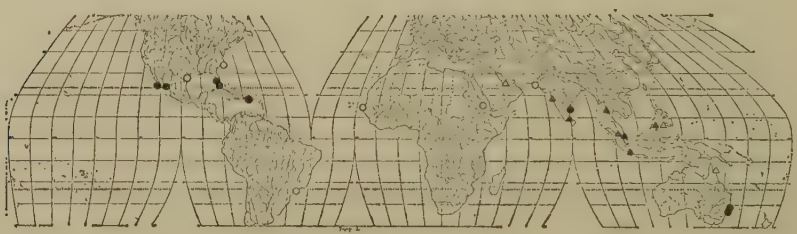
situated posterior to a transverse line drawn between posterior margin of orbits; labial furrows absent.

Origin of first dorsal fin above or slightly anterior to axil of pectoral fin, a perpendicular line drawn ventrally from origin usually intersecting axil; fifth gill slit situated distinctly behind, and fourth gill slit above (or very slightly posterior to) insertion of pectoral fin; posterior lobe of first dorsal fin terminating well anterior to insertion of pelvic fin; first through fourth gill slits nearly equal in length, and all longer than fifth gill slit; first dorsal fin relatively slender, not perfectly erect, a line drawn perpendicularly from apex of fin intersecting free rear margin of fin (posterior lobe) about halfway along its length; base of first dorsal fin about three-fifths head length and almost twice length of pectoral fin base; anterior margin of first dorsal fin nearly straight, slightly curved near apex; upper half of distal margin of first dorsal fin straight, the lower half falcate; lobe of first dorsal fin (free posterior margin) slightly less than one-half length of base; origin of second dorsal fin situated over posterior third of anal base; second dorsal fin moderately tall, its greatest height five-eighths to five-sevenths as long as base, and about five-sevenths greatest height of anal fin; second dorsal fin base about four-sevenths length of anal base; lobe of second dorsal fin long, its length about twice greatest height of fin, and extending almost to upper precaudal pit; anterior margin of pectoral fin three-fourths to four-fifths length of head, and about equal to greatest height of first dorsal; pectoral fin about three-fifths as broad as long; pectoral fin base four-fifths to seven-eighths length of anal fin base; anterior margin of pectoral slightly convex; distal margin of pectoral slightly falcate; apex of pectoral pointed; inner corner of pectoral narrowly rounded; pelvic fin about five-sixths length of anal fin; anal fin base slightly longer than pectoral and pelvic bases and more than 1½ times as long as second dorsal fin base; height of anal fin about two-sevenths again as much as height of second dorsal fin; anal fin deeply falcate toward apex and nearly straight toward tip of lobe; length of caudal fin about one-third of TL; upper margin of caudal slightly convex; terminal part of caudal about two-ninths of total length of fin; posterior margin of terminal part of caudal fin shallowly falcate; terminal apex of caudal broadly pointed; lower lobe of caudal moderately narrow and short; length of lower caudal lobe one-third to two-fifths as long as upper lobe; lower caudal lobe not erect, sloping posteriorly at about a 35° angle from a perpendicular to the body axis; anterior margin of lower caudal lobe convex; posterior margin of lower caudal lobe nearly straight; lower precaudal pit absent.

Anterior margin of rostral node of chondrocranium straight; accessory rostral cartilages absent; anterior fontanelle (viewed ventrally)

appearing extremely broad and shallowly U-shaped, with a shallow, broad, median notch; small, pointed wings present on sides of rostral node; anterior wing of olfactory cartilage prominent, pointed, and projecting medially; anterior part of preorbital process long and slender; posterior part of preorbital process terminating in an angular knob.

Teeth $\frac{15\text{–}0\text{–}16}{14\text{–}1\text{–}14}$ (one specimen examined); teeth not serrated; teeth in both jaws notably oblique, with none (except the median tooth) perfectly erect, the teeth becoming progressively more oblique toward corners of mouth, and those nearest the corners having cusps pointing almost straight back; cusps visible on all teeth, although those near corner of mouth in lower jaw poorly developed; teeth 6 through 10 in upper jaw notably larger than others; tooth 1 notably smaller than tooth 2 in lower jaw; teeth 2 through 10 in lower jaw gradually increasing in size.



MAP 1.—Distribution of species.
▲ *Sphyrna blochii* ● *Sphyrna mokarran*
(Solid=specimens examined; hollow=confirmed literature references.)

Dermal denticles (examined from upper part of back beneath first dorsal fin) not closely overlapping, the blades steeply raised; length of denticle (measured to tip of median marginal "tooth") as great, or nearly as great, as width; five strong ridges usually present, and as many bluntly pointed teeth usually present on posterior margin of denticle, the outer ridges and teeth sometimes rudimentary or absent, particularly in small individuals; median tooth on denticle ordinarily slightly longer than more distal teeth; pedicel short and broad.

Individuals gray or grayish brown dorsally, becoming more pale below; no markings on fins.

Maximum total length not recorded, possibly not more than several feet.

RANGE.—*Sphyrna blochii* is restricted to the Indo-West Pacific area and is one of the two species of hammerheads not found in the Western Hemisphere. It is known from the Persian Gulf (Blegvad and Løppenthin, 1944, p. 41, fig. 12) eastward throughout the East Indies,

and north to southern China and the southern Philippines (Herre, 1930, p. 142). The species also has been recorded from Queensland, Australia (Ogilby, 1908, p. 4); this area apparently represents both the eastern and southern limits of its range.

Sphyrna blochii, while perhaps not as closely restricted to continental waters as *Sphyrna tiburo*, nevertheless appears to be incapable of traversing broad stretches of ocean, as evidenced by its absence from outlying oceanic islands (map 1).

Subgenus *Sphyrna* Rafinesque

The subgenus *Sphyrna*, which includes *S. zygaena*, *S. lewini*, *S. couardi*, and *S. mokarran*, is distinguished by only two unique characters. These are: A large orbit, the greatest horizontal diameter greater than distance from anterior margin of orbit to narial opening; and a large maximum size, individuals reaching a size of from 12 to 20 feet in total length.

The subgenus is also distinguished by: A moderately expanded head, the greatest width from 22.9 to 30.2 percent of total body length (in specimens less than 1,000 mm. TL); first through fourth gill slits nearly equal in length, and all somewhat longer than fifth gill slit; anal fin and anal fin base relatively short, the former not over 11.0 percent, and the latter not over 7.5 percent, of TL; fifth gill slit situated distinctly behind, and fourth gill slit above (or very slightly anterior to) insertion of pectoral fin; presence of a deep narial depression; absence of an outer narial groove; lobe of first dorsal fin terminating well anterior to insertion of pelvic fin; total number of vertebrae ranging from 174 to 206 (usually 190 or more), with those over posterior part of coelomic cavity not expanded in size.

Sphyrna (*Sphyrna*) *mokarran* (Rüppell)

FIGURES 6, 7, 21*b*, 22*b*, Plates 2, 6A

?*Squalus tiburo* (misidentification) Risso, 1810, p. 35. (Identification by description of head and reference to Lacepede, "Squale pantouflier"; Nice; very rare.)

Zygaena tudes Valenciennes, 1822, pp. 225–226. (In part; original description; illustration of head; type specimens apparently represent more than one species; types from Mediterranean Sea, Cayenne, and Coromandel; specific name *tudes* subsequently restricted to a species other than one here called *Sphyrna mokarran*.)

Sphyrnichthys zygaena (misidentification) Thienemann, 1828, p. 408. (General; identification probable because teeth described as "gezähnelte.")

Zygaena mokarran Rüppell, 1835, pp. 66–67. (Original description; figures of head, teeth, and body; type specimen, a male 2510 mm. TL, Senckenberg Museum no. 3590; type locality, Massaua, Red Sea.)

Sphyrna malleus (misidentification) L. Agassiz, 1838, pp. 235, 303. (Identification probable because teeth serrate.)

Sphyrna mokarran Müller and Henle, 1841, p. 54. (Red Sea.)

Sphyrna tudes Müller and Henle, 1841, p. 53. (In part; identification from reference to Valencennes, 1822.)

?*Sphyrna chiereghini* Nardo, 1847, p. 111. (Name only.)

Sphyrnias mokarran Gray, 1851, p. 50. (In part; identification by reference to Valenciennes, 1822.)

Sphyrnias tudes Gray, 1851, p. 50. (In part; identification by reference to Valenciennes, 1822.)

Cestracion (*Zygaena*) *mokarran* Duméril, 1865, p. 383. (Compiled.)

Cestracion (*Zygaena*) *tudes* Duméril, 1865, p. 384. (In part; description from Valenciennes, 1822.)

Squalus zygaena (misidentification) de la Blanchere, 1868, p. 499. (Teeth described as "dentelees.")

Cestracion tudes Ninni, 1872, p. 10. (Not seen.)

Cestracion mokarran Bleeker, 1873, p. 115. (Chinese drawing.)

Zygaena dissimilis Murray, 1887, p. 103. (Original description; type locality, Kurrachee.)

Sphyrna (*Platysqualus*) *tudes* Jordan and Evermann, 1896, p. 217. (Name; West Indies and Mediterranean; references to specimens from Gulf of California and Indian Ocean perhaps do not pertain to this species.)

Cestracion zygaena (misidentification) Radcliffe, 1916, p. 263. (Identification by description of teeth in illustration as serrate; specimens 12 ft., 6 in. long; Beaufort, N.C.)

Sphyrna zygaena (misidentification in part) Coles, 1919, p. 41. (Identification by shape of head in photo, of 13 ft., 10 in. female; Cape Lookout, N.C.)

Platysqualus tudes Howell-Rivero, 1936, p. 44. (Identification probable because of large size, 12 to 14 ft.; Cuba.)

Sphyrna lewini (misidentification in part) Fowler, 1941, p. 215. (Figure of *S. mokarran* incorrectly labelled *S. lewini*.)

Sphyrna ligo Fraser-Brunner, 1950, pp. 213–219. (Original description; figure; holotype, an embryo, BMNH 1890.9.23.231; type locality, Clarence River, New South Wales, Australia; radiograph of head seen.)

Specimens examined.—(Range in size: 435–675 mm. TL; heads of larger specimens also examined). Atlantic Ocean: Senegal: (photograph seen), Gorée. United States (Florida): USNM 106543 (1), USNM 108453 (1), USNM 108454 (1), FMNH 63092 (1), MCZ 35247 (1), SU 14330 (1), Englewood; FMNH 530, Captiva Pass; USNM 186087 (2), 25°56′ N., 81°47′ W.

Pacific Ocean: Australia: USNM 40014 (1), USNM 40026 (1), MCZ 969 (1), Richmond River, New South Wales; BMNH 1890.9.23. 231 (x-ray of head of holotype of *Sphyrna ligo*), Clarence River, New South Wales. India: USNM 12622 (1), Madras. Mexico: USNM 29645 (1), USNM 37162 (1), Mazatlan; UCLA 52–252 (1), Bahia Almejas, Isla Santa Margarita, Baja California.

Nomenclature.—*Zygaena mokarran* was described by Rüppell (1835, pp. 66–67, pl. 17, fig. 3) from the Red Sea, at Massaua. The illustration (pl. 2), though inaccurate in certain details, particularly the conformation of the fins, is readily identified by the shape of the head. In addition, the type specimen (Senckenberg Museum no. 3590) has been illustrated recently by Klausewitz (1960, p. 293).

For many years the species herein called *Sphyrna mokarran* was known as *Sphyrna tudes*. Tortonese (1950b, pp. 1030–1033) was the first to point out that the three type specimens of *Zygaena tudes* actually comprise two species, one of which may be *S. mokarran*. Only two of the types are apparently now extant (one from Nice, France; the second from Cayenne, French Guiana), neither of which is *S. mokarran*. However, since the missing specimen is from an area (Coromandel, India) where the species represented by the two existing types does not occur, and since there is a fairly close superficial resemblance between the two species in question, one can assume that the Coromandel individual was probably *Sphyrna mokarran*.

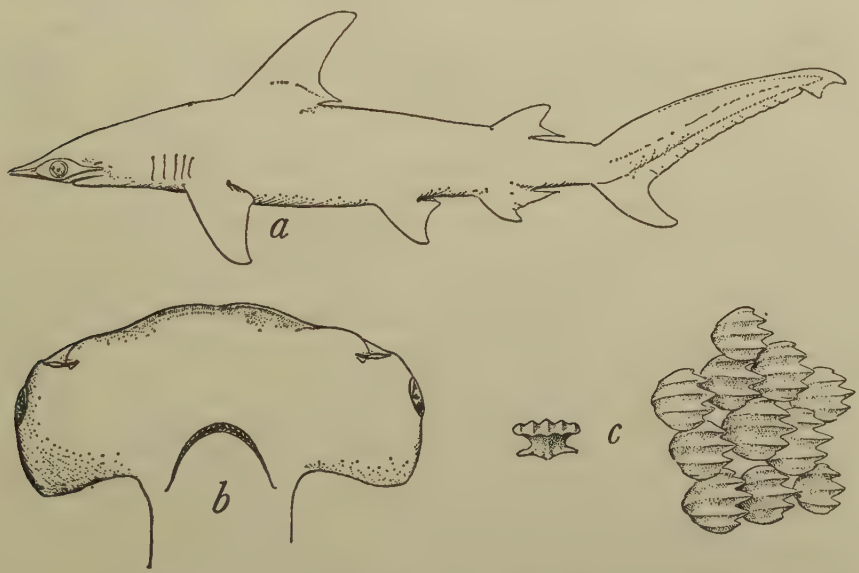


FIGURE 6.—*Sphyrna mokarran*: *a*, juvenile male, 673 mm. TL, from Englewood, Fla. (USNM 106543); *b*, head, 0.2 × (USNM 106543); *c*, dermal denticles, about 49 × (USNM 106543). (From Bigelow and Schroeder, 1948, p. 430.)

DIAGNOSIS.—Characters mentioned in the diagnosis of the subgenus *Sphyrna* are not repeated here.

Sphyrna mokarran is unique among members of the genus *Sphyrna* in having a deeply falcate pelvic fin and strongly serrated teeth at all sizes. *S. mokarran* is also characterized by a deep median indentation (scallop) on anterior margin of head; absence of an inner narial groove, this structure represented by a thin line; a tall second dorsal fin, the height of the fin slightly greater than height of anal fin; a short second dorsal lobe, the length of the lobe equal to height of fin and extending only about one-half of distance from posterior part of fin base to upper

precaudal pit; a shallow upper precaudal pit, with an acutely pointed posterior ridge to upper precaudal pit (fig. 21*b*); an anterior-median pore patch in which the outer-posterior corners are sharply angled and the posterior edge is straight (fig. 22*b*); presence of a rostral fenestra, and several other chondrocranial characters (pl. 6A).

A comparison of *S. mokarran* with other members of the genus is presented in table 1.

DESCRIPTION.—Meristic data appear in table 3. Characters mentioned in the diagnoses of the subgenus *Sphyrna* and *S. mokarran* are not repeated here.

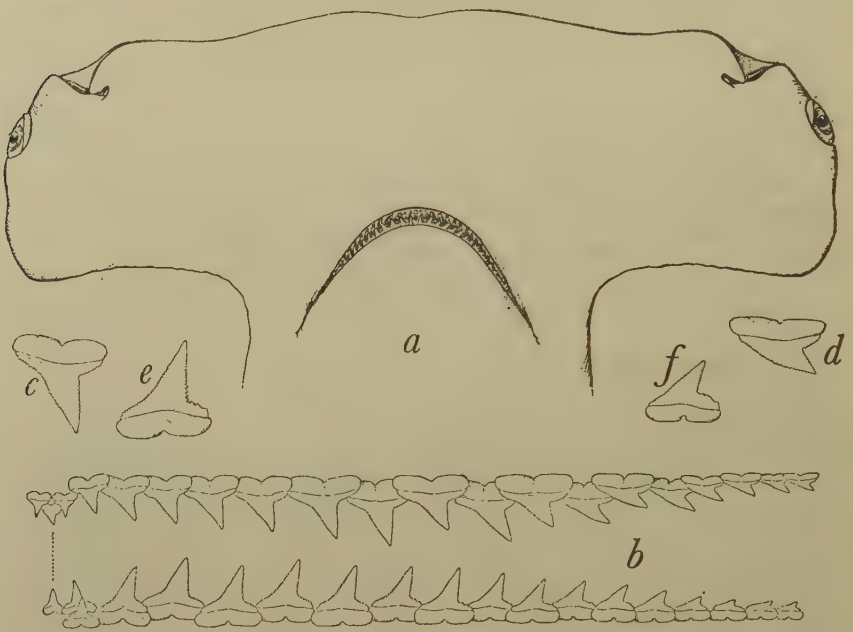


FIGURE 7.—*Sphyrna mokarran*: *a*, head of small adult, 1,660 mm. TL, from Englewood, Fla., 0.09 × natural size (USNM 108453); *b*, teeth series from left side of upper and lower jaws (USNM 108453), about natural size; *c*, fifth upper tooth; *d*, twelfth upper tooth; *e*, fifth lower tooth; *f*, eleventh lower tooth. (*c-f*, about 1.5 ×.) (From Bigelow and Schroeder, 1948, p. 429.)

Head moderately expanded, the greatest width from 22.9 to 27.3 percent of TL (in specimens less than 1,000 mm. long); shallow scallops present on anterior margin of head about halfway between nares and tip of snout; outer posterior corner of lateral expansion of head posterior to corner of mouth in smaller specimens, anterior to corner of mouth in larger individuals; narial flap broad, broadly pointed at tip, with the outer edge curving abruptly inward; orbit large, the horizontal diameter almost equal to length of shortest (fifth) gill slit;

length of snout from one-third to one-fourth of head width; greatest transverse distance between corners of mouth about one-fourth of greatest width of head; symphysis of jaws situated posterior to a transverse line drawn between posterior margins of orbits; labial furrows absent.

Origin of first dorsal fin above axil of pectoral fin, a perpendicular line drawn ventrally from origin intersecting at, or slightly behind, this point; first dorsal fin tall, slender, and pointing strongly posteriorly, a line drawn perpendicularly from apex of fin passing well back of fin lobe; base of first dorsal fin slightly less than one-half head length and almost twice length of pectoral fin base; anterior margin of first dorsal fin broadly curved (excessively curved in embryonic and early post-embryonic individuals); upper two-thirds of distal margin of first dorsal fin straight or slightly falcate toward tip, the lower one-third distinctly falcate; lobe of first dorsal fin about one-third length of base; origin of second dorsal fin situated slightly behind origin of anal fin; second dorsal fin base slightly greater than four-fifths length of anal fin base; anterior margin of pectoral fin slightly longer than one-half length of head and a little less than greatest vertical height of first dorsal fin; pectoral fin two-thirds as broad as long; pectoral fin base about four-fifths length of anal fin base; anterior margin of pectoral broadly rounded (strongly curved in embryos and early post-embryos); distal margin of pectoral broadly falcate; apex of pectoral broadly pointed; inner corner of pectoral broadly rounded; length of pelvic fin almost equal to length of anal fin; pelvic fin base slightly less than length of anal base; anterior margin of pelvic nearly straight, except near apex, where it is broadly curved; length of anal fin slightly greater than length of pelvic fin; anal fin base slightly (up to one-sixth) longer than pectoral, pelvic, and second dorsal fin bases; anal fin deeply falcate toward apex, nearly straight toward tip of lobe; length of caudal fin nearly a third of TL; upper margin of caudal slightly convex; terminal part of caudal about one-fourth of total length of fin; posterior margin of terminal part of caudal fin notably falcate; terminal apex of caudal broadly pointed; lower lobe of caudal narrow and long, the distance from angle included by the upper and lower caudal lobes to tip of latter going about 2½ times in anterior margin of lower caudal lobe; length of lower caudal lobe one-third to two-fifths as long as upper lobe; lower caudal lobe not erect, sloping posteriorly at about a 45° angle from a perpendicular to body axis; anterior margin of lower caudal lobe convex; posterior margin of lower caudal lobe nearly straight or slightly concave.

Anterior margin of rostral node of chondrocranium straight; accessory rostral cartilages absent; anterior fontanelle (viewed ventrally) shallow and nearly straight on posterior margin; prominent,

broad, bluntly rounded wings present on sides of rostral node; no anterior wing on olfactory cartilage; tip of anterior part of preorbital process very short, blunt, and rather thick; posterior part of preorbital process terminating in an evenly rounded knob.

Total number of vertebrae 205 to 206 (in two specimens examined); body vertebrae 95 to 98, there being from 10 to 11 fewer body than caudal vertebrae.

Teeth $\frac{17\text{–}2 \text{ or } 3\text{–}17}{16 \text{ or } 17\text{–}1 \text{ to } 3\text{–}16 \text{ or } 17}$; upper teeth triangular, on expanded bases, the first tooth erect, symmetrical, but the subsequent upper teeth increasingly oblique toward corners of mouth; second to tenth or eleventh teeth the largest in both upper and lower jaws; outermost teeth in both jaws with distinct cusps; one or two series of teeth functional in alternating rows along sides of upper jaw and usually two rows along sides of lower jaw.

Dermal denticles (examined from upper part of back beneath first dorsal fin) evenly and closely spaced, but with skin often visible in between, the blades thin and little arched; length of denticle (measured to tip of median marginal "tooth") about same as width; small specimens with from three to five, larger specimens with five or even six, smooth-topped ridges, and as many short, broadly pointed marginal teeth on dermal denticle; median tooth on denticle slightly longer than more distal teeth; pedicel short and thick.

Individuals with gray or grayish brown dorsally, becoming more pale below; no markings on fins.

Maximum total length reputedly about 20 feet.

Variation.—Comparatively few specimens of *Sphyrna mokarran* were available for study, and of these a large percentage (including all individuals from the Indo-Pacific region) were very small embryos. Specimens of this species are characterized by strongly curled bodies at this stage of development, and this, together with the paucity of specimens, tends to negate apparent differences, such as orbital diameter and length of second dorsal fin base, between specimens from the Atlantic and Pacific regions (table 3). In addition, radiographs of the chondrocrania show no apparent differences. For these reasons, as well as the fact that neither of the other hammerheads of worldwide distribution (*S. zygaena* and *S. lewini*) show any noticeable intraspecific differentiation, it seems best to recognize but one species, *Sphyrna mokarran*.

Range.—*Sphyrna mokarran* is circumtropical in distribution (map 1). However, it does not usually appear to be as common as *Sphyrna lewini*, a species occupying a similar range.

S. mokarran is found in the western Atlantic, including the Gulf of Mexico and Caribbean Sea, from North Carolina south to Brazil.

It is present in the eastern Atlantic, at least off the northwest coast of Africa (Cadenat, 1951, pp. 96–97) and in the Red Sea. Despite its presence in the last two areas, there are no substantiated records from the intervening Mediterranean (Tortonese, 1950a, p. 36). This is probably not due to lack of adequate collecting, as certain other species, such as the carcharhinid shark *Rhizoprionodon acutus* (Victor G. Springer, pers. comm.), show a similar hiatus in distribution.

Sphyrna mokarran is present in the eastern Pacific from the Gulf of California south to Panama and probably northwestern South America. It occurs in the Pacific from southern Japan south to Australia, although it appears to be absent from New Zealand and the more eastern parts of Oceania. *S. mokarran* is found throughout the East Indies and westward, in the northern Indian Ocean, to east Africa.

Sphyrna (Sphyrna) zygaena (Linnaeus)

FIGURES 8, 9, 21*c*, 22*c*; PLATE 6C

Squalus zygaena Linnaeus, 1758, p. 234. (By reference to illustration by Willughby, 1686; no type specimen; type locality, "Europe," "America.")

Squalus zygena Bonnaterre, 1788, p. 9. (Atlantic and Mediterranean.)

Sphyrna zygaena Rafinesque, 1810, p. 46. (Identification by included references; Sicily.)

?*Cestrorhinus caroliniensis* Blainville, 1816, p. 121. (Name only.)

?*Cestrorhinus pictus* Blainville, 1816, p. 121. (Name only.)

Zygaena zygaena Cuvier, 1817, p. 127. (General; identification by references.)

Zygaena malleus Valenciennes, 1822, p. 223. ("French" coasts; Brazil.)

Zygaena vulgaris Cloquet, 1830, p. 621. (At least in part; general.)

Zygaena subarcuata Storer, 1848, p. 70. (Identified by description of 2 ft. specimen; type presumably in MCZ [not located]; type locality, Provincetown, Cape Cod.)

Sphyrnias zygaena Gray, 1851, p. 48. (In part; identification by references, but also includes *lewini* [misspelled *"lewisii"*].)

Sphyrna malleus van der Hoeven, 1855, p. 262. (General; Mediterranean; identification by reference to Linnaeus.)

Cestracion zygaena Gill, 1861, p. 403. (Name only; identification by reference to Linnaeus, 1758.)

Cestracion subarcuata Gill, 1862, p. 59. (Name only; evidently based on *Zygaena subarcuata* Storer, 1848.)

?*Cestracyon zygaena* Poey, 1881, p. 348. (Refers primarily to *Sphyrna lewini;* specimens from Mediterranean may apply in part to *S. zygaena.*)

?*Zygoena malleus* Sauvage, 1891, p. 510. (May refer entirely or in part to *Sphyrna lewini.*)

?*Sphyrna* (*Zygaena*) *zygaena* Imms, 1905, p. 43. (Pharyngeal denticles; name only; may refer entirely or in part to *S. lewini.*)

?*Sphyrna* (*Sphyrna*) *zygaena* McCulloch and Whitley, 1925, p. 129. (Reference; may refer in part to *S. lewini.*)

Sphyrna (*Cestracion*) *zygaena* von Bonde, 1933, p. 377. (South Africa; skull and nerves; identification by photo of head.)

Zygaena zigaena Nobre, 1935, p. 425. (Portugal; identification by description of head.)

SPECIMENS EXAMINED.—(Range in size: 457–2,663 mm. TL). Atlantic Ocean (including Mediterranean Sea): Azores: USNM 94502 (1), Terceira. Brazil: MCZ 451 (1), MCZ 35364–35365 (2), Rio de Janeiro. Italy: USNM 28452 (1), Livorno; ANSP 604 (1), (no further data). United States (Florida): UMML 5639 (head), off Alligator Reef, Monroe Co.; UMML 10444 (1), off North Miami, Dade Co. (in Gulf Stream). (Massachusetts): USNM 10418 (1), USNM 83980 (1), Woods Hole; MCZ 36425 (1), USNM 33268 (1), Buzzards Bay, Woods Hole; USNM 31527 (1), Stuart's Pond, Buzzards Bay; MCZ 1159 (1), Nahant; MCZ 1416 (1), Cape Cod. (Maryland): USNM 76681–76683 (3), Ocean City. (New Jersey): USNM 93845 (3), USNM 120495 (11), Barnegat Bay, Seaside Park; ANSP 522 (1), Holly Beach. (New York): CAS 19189 (1), Graves End Bay; USNM 116447 (5), Sandy Hook; UMMZ 115903 (1), Long Island; MCZ 136 (2), no further data. (Virginia): USNM 119699 (1), off Virginia Beach; USNM 6090 (1), Norfolk.

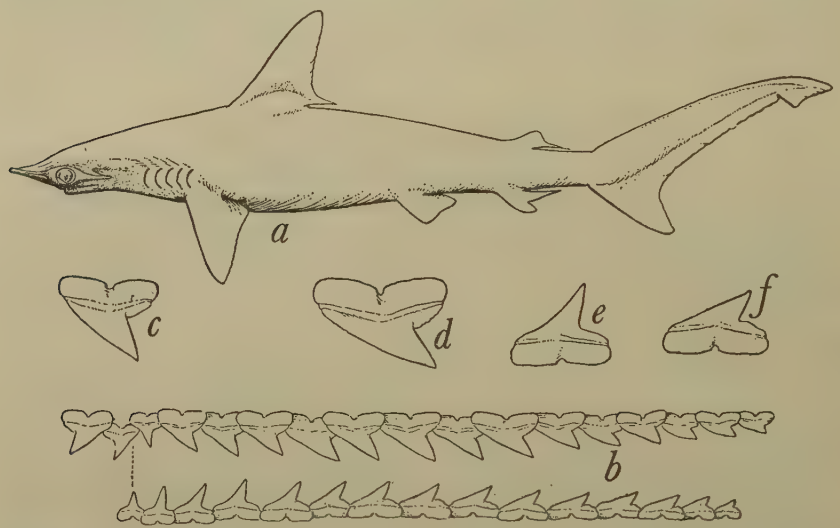


FIGURE 8.—*Sphyrna zygaena: a*, juvenile female, 687 mm. TL, from Nahant, Mass. (MCZ 1159); *b*, upper and lower teeth, left side, about 1.7 ×; *c*, second upper tooth; *d*, ninth upper tooth; *e*, third lower tooth; *f*, ninth lower tooth. (*c-f*, about 3.8 ×.) (From Bigelow and Schroeder, 1948, p. 437.)

Pacific Ocean: Australia: USNM 29020 (head), USNM 39992 (1), Sydney (Port Jackson). Ecuador: USNM 127758 (head), Gulf of Guayaquil, 81°13′ W., 4°13′ S.; MCZ 383 (1), Galapagos Islands. Japan: USNM 23383 (stuffed skin), USNM 71779 (1), Tokyo market;

USNM 51289 (head), Wakanoura; USNM 51291 (head), Nagasaki; FMNH 57423 (1), Osaka market; MCZ 1042 (1), Yenoshima; SU 24125 (1), Misaki; UMMZ 179078 (1), vicinity of Choshi; UMMZ 179079 (1), Hakata Bay, northern Kyushu; UMMZ 179080 (1), Suruga Bay. Mexico: USNM 190592 (10), Gulf of California, southern end of Angel de la Guarda Island; UMMZ 61032 (1), Cedros Island. New Zealand: UMML uncataloged (2), Bay of Islands, North Island. Panama: MCZ 515 (1), no further data. Peru: USNM 77711 (head), I. Lobos de Tierra; MCZ 421 (1), MCZ 441 (3), Magdalena Bay; MCZ 382 (2), Payta; SIO 58–29 (1), "off Peru"; SU 13003 (1), no further data. United States (California): SIO 58–224, SIO 58–382 (jaws), off La Jolla, San Diego County; LACM uncataloged (jaws and chondrocranium), off San Diego.

DIAGNOSIS.—Characters mentioned in the diagnosis of the subgenus *Sphyrna* are not repeated here.

Sphyrna zygaena is characterized (as is *S. lewini*, its closest relative) by a long second dorsal fin lobe and a low second dorsal fin, the length of the former about twice greatest height of fin. The anterior-median pore patch on the underside of the head is unique, the patch characterized by a broad, smoothly rounded angle at the outer-posterior corner and a broad, pointed posterior extension in the median-posterior area (fig. 22*c*).

S. zygaena is distinguished from *S. lewini* by lack of a median indentation (scallop) on anterior margin of head; a longer inner narial groove, which extends at least 50 percent of distance from inner margin of nares to tip of snout; orbit closer to nares, being separated by a distance equal to about half of greatest horizontal diameter of eye; tip of second dorsal lobe not reaching as near to upper precaudal pit, the lobe extending, at most, about two-thirds of distance from second dorsal base to pit; a slightly more deeply falcate anal fin, the deepest part of the notch on the distal margin situated slightly posterior to a line drawn perpendicularly from the posterior axil of the fin; a shorter anal base, the length of which is slightly less than length of pectoral base; a more acutely pointed posterior ridge to the upper precaudal pit (fig. 21*c*); absence of a lower precaudal pit; absence of a rostral fenestra; and several other chondrocranial characters (pl. 6c).

A comparison of *Sphyrna zygaena* with other members of the genus *Sphyrna* is presented in table 1.

DESCRIPTION.—Meristic data appear in table 4. Characters mentioned in the diagnoses of the subgenus *Sphyrna* and of *S. zygaena* are not repeated here.

Head moderately expanded, the greatest width from 26.1 to 29.0 percent of TL (in specimens less than 1,000 mm. long); shallow

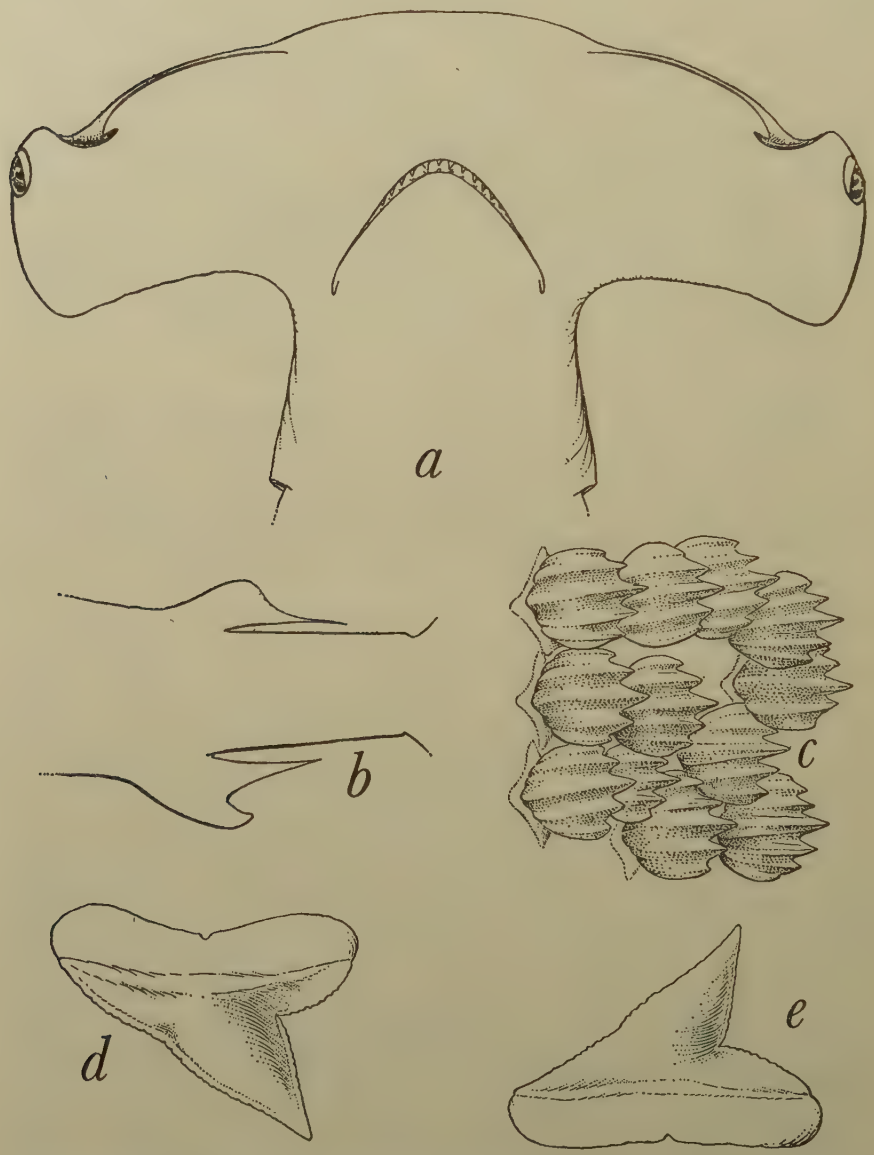


FIGURE 9.—*Sphyrna zygaena: a*, head of specimen illustrated in figure 8 (MCZ 1159), ventral view, about 0.45 × natural size; *b*, second dorsal and anal fins; *c*, dermal denticles, about 45 ×; *d*, fourth upper tooth; *e*, fifth lower tooth. (*d-e*, about 9 ×.) (From Bigelow and Schroeder, 1948, p. 438.)

scallops present on anterior margin of head, about halfway between nares and tip of snout; outer posterior corner of lateral expansion of head posterior to corner of mouth, probably in specimens of all sizes; narial flap broad, moderately pointed at tip, with the outer edge curving evenly inward; orbit large, the horizontal diameter about equal to length of longest (second) gill slit; length of snout from one-fifth to one-fourth of head width; greatest transverse distance between corners of mouth from one-fifth to one-fourth of greatest width of head; symphysis of jaws situated posterior to a transverse line drawn between posterior margins of orbits in specimens of all sizes; labial furrow present at corners of lower jaw only (concealed when mouth is closed), about one-fifth as long as greatest horizontal diameter of eye.

Origin of first dorsal fin above posterior axil of pectoral fin, a perpendicular line drawn ventrally from origin intersecting axil; first dorsal fin broad, rather erect (not as erect as in large examples of *Sphyrna tudes*), a line drawn perpendicularly from apex of fin passing close behind base; base of first dorsal fin from two-fifths to nine-twentieths of length of head, and from three-fourths again to nearly twice length of pectoral fin base; anterior margin of first dorsal fin evenly curved, with the part nearest the apex very strongly curved; distal margin of first dorsal fin strongly falcate; lobe of first dorsal fin about one-third length of base; origin of second dorsal fin situated about halfway back above base of anal fin; second dorsal fin base from three-fifths to four-fifths length of anal fin base; anterior margin of pectoral fin from one-half to two-thirds length of head (higher values usually apply to larger individuals) and about equal to or slightly greater than greatest vertical height of first dorsal fin; pectoral fin about two-thirds as broad as long; anterior margin of pectoral moderately convex; distal margin of pectoral slightly falcate; apex and inner corner of pectoral rounded; length of pelvic fin about four-fifths length of anal fin; length of pelvic fin base approximately equal to length of anal fin base; anterior margin of pelvic fin weakly convex, the distal margin nearly straight; length of anal fin equal to or slightly greater than length of pelvic fin; height of anal fin about a third again as much as height of second dorsal; length of caudal fin nearly a third of TL; upper margin of caudal fin nearly straight; terminal part of caudal about one-fifth of total length of fin; posterior margin of terminal part of caudal fin moderately falcate; terminal apex of caudal narrowly rounded; lower lobe of caudal relatively narrow and long, the distance from angle included by upper and lower caudal lobes to tip of latter going about twice in anterior margin of lower caudal lobe; length of lower caudal lobe one-third to two-fifths as long as upper lobe; lower caudal fairly erect, sloping posteriorly at about a 35° angle from a

perpendicular to the body axis; anterior margin of lower caudal lobe weakly convex; posterior margin of lower caudal lobe nearly straight.

Anterior margin of rostral node of chondrocranium nearly straight, or with a broad, very shallow median indentation; accessory rostral cartilages absent; anterior fontanelle (viewed ventrally) rather deep and evenly rounded, with no noticeable median notch; short, rounded wings present on sides of rostral node; anterior wing of olfactory cartilage absent, represented only by a small "bump"; anterior part of preorbital process long and slender, and without a sharp angle on anterior edge; posterior part of preorbital process terminating in an evenly rounded knob.

Total number of vertebrae 196 (in one specimen examined); body vertebrae 101, there being six more body than caudal vertebrae.

Teeth $\frac{13 \text{ to } 15\text{–}0 \text{ or } 1\text{–}13 \text{ to } 15}{12 \text{ to } 14\text{–}1\text{–}12 \text{ to } 14}$; teeth weakly serrate in large individuals; first upper tooth nearly symmetrical and erect; subsequent upper teeth strongly oblique, their inner margins straight or evenly convex, their outer margins deeply incised and with the outermost teeth with very small, though well-developed cusps; lower teeth similar to upper, though smaller; first four teeth in lower jaw rather erect and with narrow cusps; one small symmetrical tooth at symphysis of lower jaw, none or one in upper jaw; one to two series of teeth functional along sides of upper jaw, and two to three series functional toward center; two to three series functional in lower jaw.

Dermal denticles (examined from upper part of back beneath first dorsal fin) closely overlapping, the blades thin and moderately arched; length of denticle (measured to tip of median marginal "tooth") as great, or nearly as great, as width; small specimens usually with three, large specimens with up to seven, sharp-toothed ridges, and from three to five pointed marginal teeth present on denticle; median tooth on denticle slightly longer than more distal teeth; pedicel very short.

Individuals deep olive to brownish gray dorsally, shading to white ventrally; tip of ventral surface of pectoral fin sometimes faintly gray black in life.

Maximum total length probably between 12 and 13 feet.

RANGE.—*Sphyrna zygaena* has an antitropical distribution, occurring in cooler waters of both the Northern and Southern Hemispheres but apparently absent from the intervening warmer areas (map 2). It is present in the western Atlantic from Nova Scotia and northern New England south to (occasionally) southern Florida (UMML 5639 and UMML 10444), and from Argentina and Uruguay to (probably) northern Brazil (exact northern limits of range in South American waters uncertain). Stewart Springer (pers. comm.) states that he

knows of no authentic record for this species from the Gulf of Mexico or Caribbean, all literature records applying to *Sphyrna lewini*, which is common there.

In the eastern Atlantic *Sphyrna zygaena* is known from Scotland south to Senegal, in northwest Africa (Cadenat, 1951, p. 46), and also from the Mediterranean Sea. Records of *S. zygaena* farther south along the coast of Africa (Irvine, 1947, pp. 89, 90) and from South Africa (Smith 1953, pp. 46, 47) may not have been based on this species, however, since in neither case were adequate descriptions given, and the hammerheads pictured represent species other than *zygaena*. Considering that the cool waters off South Africa are suitable for *S. zygaena*, however, it is likely that the species does occur there.

MAP 2.—Distribution of *Sphyrna zygaena*.
(Solid=specimens examined; hollow=confirmed literature references.)

In the eastern Pacific *Sphyrna zygaena* is known from western South America (Chile, Peru, and the Galapagos Islands) and (one record) Panama, and from southern California and Mexico (south to the Gulf of California), but intensive collecting has failed to reveal its presence between the above two areas. In the northwestern Pacific *S. zygaena* is common around southern Japan, although the exact northern limits of its range there are uncertain. It seems to be absent from the Hawaiian Islands and the East Indian area, but is present off New Zealand and southern Australia. It probably is also present in the southern parts of the Indian Ocean as well.

Sphyrna (*Sphyrna*) *lewini* (Griffith and Smith)

FIGURES 10, 21*d*, 22*d*; PLATES 3, 6B, 9B, 10B

?*Cestrorhinus caroliniensis* Blainville, 1816, p. 121. (Name only.)

?*Cestrorhinus pictus* Blainville, 1816, p. 121. (Name only.)

Zygaena malleus Valenciennes, 1822, p. 223. (In part; description; illustration of head; Mediterranean Sea and Atlantic Ocean; teeth described as denticulate.)

?*Zygaena indica* Van Hasselt, 1823, p. 315. (Type locality: Java.)

Zygaena lewini Griffith and Smith, *in* Cuvier, Griffith, and Smith, Animal Kingdom, vol. 10, p. 640, pl. 50, 1834. (Original description; figure; no type specimen; type locality, south coast of New Holland.)

Sphyrnias zygaena (misidentification in part) Gray, 1851, p. 48. (In part; *malleus* included in synonymy.)

Sphyrna lewini Duméril, 1858, p. 261. (Possibly in part; Gorrée, West Africa.)

Cestracion leeuwenii Day, 1865, p. 271. (Description; Malabar; distinguished from *C. zygaena*.)

Cestracion (*Zygaena*) *leeuwenii* Duméril, 1865, p. 383. ("Cotes de la terre de Leeuwen" [Australia].)

?*Cestracion* (*Sphyrna*) *zygaena* (misidentification) Steindachner, 1870, p. 576. (Possibly in part; name only; Senegambia.)

Zygaena erythraea (Ehrenberg) Klunzinger, 1871, p. 666. (Name in synonymy.)

Zygaena leuwinii Ramsay, 1881, p. 96. (Possibly in part; name only; Port Jackson, Australia.)

Cestracyon zygaena (misidentification) Poey, 1881, p. 348. (Porto Rico, Guiana, Mediterranean area, East Indies; refers primarily to *Sphyrna lewini;* specimens from Mediterranean may apply in part to *S. zygaena*.)

?*Sphyrna zygaena* (possible misidentification) Studer, 1889, p. 263. (Moreton Bay.)

?*Zygoena malleus* (possible misidentification) Sauvage, 1891, p. 510. (May refer entirely or in part to *Sphyrna zygaena*.)

?*Sphyrna* (*Zygaena*) *zygaena* (possible misidentification) Imms, 1905, p. 43. (Pharyngeal denticles; name only; may refer entirely or in part to *Sphyrna zygaena*.)

?*Sphyrna tudes* (possible misidentification) Ogilby, 1908, p. 4. (May refer to *Sphyrna mokarran*.)

Cestracion oceanica Garman, 1913, pp. 158–159. (Original description; type locality, Society Islands.)

Cestracion lewini Ogilby, 1916, pp. 81, 94. (Moreton Bay, Queensland.)

Sphyrna (*Sphyrna*) *lewini* McCulloch and Whitley, 1925, p. 129. (Reference.)

?*Sphyrna* (*Sphyrna*) *zygaena* (possible misidentification) McCulloch and Whitley, 1925, p. 129. (May refer in part to *Sphyrna lewini*.)

Sphyrna oceanica Fowler, 1928, p. 23. (Copied.)

Cestracion zygoena (probable misidentification) Chevey, 1932, p. 6. (Cochin China; misidentification probable because of locality.)

Sphyrna diplana Springer, 1941, pp. 46–52. (Original description; type locality, Englewood, Fla.)

Specimens examined.—(Range in size: 386–1,755 mm. TL). Atlantic Ocean: "Atlantic": MCZ 393 (1), no further data. "Europe": MCZ 673 (1), no further data. "West Indies": SU 11830 (1), no further data. Bahamas: UMML 10867 (1), off west end Grand Bahamas Island. Brazil: MCZ 462 (4), Rio de Janeiro; MCZ 314 (1), MCZ 470 (1), SU 52717–52719 (3), Rio Grande do Sul; SU 52874 (1), Florianopolis; SU 14046 (1), Santos. Cuba: USNM 111350 (chondrocranium), no further data. Italy: UP uncataloged (1), Livorno. Guinea: USNM uncataloged (1, head and fins), 9° 34′ N., 16° 18′ W. Jamaica: USNM 29999 (1), no further data. Liberia: USNM 179705–179706 (2), Messurado River beach. Mexico: MCZ 39646 (1), off Ciudad Carmen, Campeche; SU 11696 (1), no further data. Panama: USNM 79282 (1), USNM 79285 (1), ANSP 49936–49937 (2 heads), Colon. Surinam: USNM 159196 (1), 06°23′ to 06°20′ N., 54°47′ to 54°51′ W.; USNM 159197 (1), USNM 159199 (1),

06°27′ to 06°25′ N., 55°05′ to 55°10′ W. Trinidad: FMNH 3165 (2), no further data; SU 19193 (1), 1°29′ N., 10°39′ W. (This locality, as listed, is not close to Trinidad.) United States (Florida): USNM 106544 (1), UMMZ 155050 (1), Englewood; USNM 108451 (holotype of *Sphyrna diplana*), Englewood; USNM 133580 (1), Merritt Island, Brevard Co.: UF 455 (1), Matanzas Inlet, St. Johns Co.; UF 4208 (1), Fernandina, Nassau Co. (Georgia): UF 5463 (1), mouth of St. Simons Sound, Glynn Co. (South Carolina): USNM 25180 (1), Charleston; USNM, 32°42′ N., 79°02′ W. (Texas): FMNH 37798 (1), Port Aransas; USNM 158561 (1), Freeport; MCZ 35223 (1) MCZ 35826–35828 (3), USNM 116449 (3), USNM 118660 (1), Galveston; SU 18390 (1), no further data.

Pacific Ocean (including Indian Ocean and Red Sea): Aden: BMNH 1925.7.20.32.37 (6), Gulf of Aden. Burma: SU 14496 (1), South Moscos Island group. Celebes: MCZ 479 (1), no further data; USNM 170557 (1), Makassar market. China: SU 14150 (1), Tinghai, Chu Shan Island; USNM 130604 (1), Foochow. Costa Rica: SIO 52–94 (1), Puntarenas. Eritrea: USNM 49330 (1), Red Sea, at Massaua. Hawaii: MCZ 471 (1), USNM 151539 (1), Honolulu; USNM 52642 (1), USNM 52644 (1), Honolulu, 28°31′00″ N., 141°47′00″ W.; SU 12765 (1), SU 14088 (1), MCZ 79 (1), MCZ 456 (1), no further data. India: SU 14398 (1), Calicut. Java: USNM 72476 (1), Batavia. Japan: UMMZ 177119 (1), Southern Chosen (South Korea?). Mexico: SU 11696 (1), no further data; USNM 120376 (head), Gulf of California, off San Marcos Island. New Caledonia: USNM 111201 (head), USNM 111243–111244 (2 dried skins), no further data. Panama: ANSP 565 (1), MCZ 517 (2), "Pacific side," no further data; USNM 29289 (1), USNM 111414 (stuffed skin), no further data; ANSP 82186 (2), San Miguel Bay, Garachine Pt.; MCZ 1063 (1), MCZ 1059–1061 (3), Panama Bay, San Miguel Island; MCZ 1088–1092 (5), Panama Bay, near Panama; UCLA 53–275 (3), Panama Bay, between Panama City and Punta Gorda. Philippines: USNM 170554 (1), Iloilo market; USNM 170555–170556 (2), Manila market; USNM 56337 (1), Cavite. Society Islands: MCZ 460 (3), USNM 153587 (1) (syntypes of *Cestracion oceanica*), no further data.

Nomenclature.—*Sphyrna lewini* was originally described (as *Zygaena lewini* Griffith and Smith, 1834, p. 640, pl. 50) from the south coast of Australia, or "New Holland," as it was then called. Although the description lists none of the important diagnostic features, the accompanying picture (pl. 3) is identifiable, and can be recognized by the distinct median indentation on the anterior part of the head and the low second dorsal fin with a long lobe.

In the past Griffith has been cited as the original describer of *Sphyrna lewini*, a circumstance resulting from the inclusion of his

name on the title page as author of the supplementary sections in the English (1834) edition of Cuvier's "The Animal Kingdom." Apparently overlooked, however, is the fact that there are actually two consecutive title pages to each volume, and, on the second page of volume 10, under the heading "The Class Pisces," the names of Edward Griffith and Charles Hamilton Smith appear, thus indicating their responsibility for the new sections on the orders of fishes. The past confusion has resulted because only Griffith's name appears on the first title page (entitled "The Animal Kingdom") as author of the additions, although the words "and others" are written in small type underneath. It is clear from the above that Cuvier had no part in the preparation of these supplements, thereby eliminating him as a codescriber of the species named therein; and therefore, Griffith and Smith should be regarded as describers of *Sphyrna lewini* and other new forms appearing in this volume.

For a long time *Sphyrna lewini* was confused with the superficially similar *S. zygaena*. Garman seems to have been the first to recognize the distinctness of the two species, since, in his monograph of the sharks (1913, pp. 158–159), he described a new hammerhead, *Cestracion oceanica*, which he noted was "closely allied to *C. zygaena*, [and] similar in most respects." In the comparison of this species with *zygaena*, reference was made to the long inner narial groove of the latter (extending more than halfway from the nares to the middle of the snout). The length of the inner narial groove in *oceanica*, together with other characters mentioned in the original description, would lead one to suspect that this species is identical with *Sphyrna lewini*, a suspicion that is confirmed by examination of the four syntypes (MCZ 460 [3 spec.]; USNM 153587 [1 spec.]). Although Garman distinguished the young of the above species, there is no evidence that he recognized the adults, a situation that is difficult to understand in view of the fact that the difference in length of the inner narial groove, which he recognized in the young, remains constant at all sizes.

Springer (1941, pp. 46–52) was the first to demonstrate conclusively that *S. zygaena* and *S. lewini* are specifically distinct. At the time, however, he was unaware that the Atlantic and Pacific populations of *lewini* are morphologically indistinguishable, and he consequently described the former population as a new species, *S. diplana*.

Tortonese (1950a, pp. 21–28), although continuing to recognize both *S. diplana* and *S. lewini*, strongly questioned their taxonomic separation. He did not synonymize the two species, however, due to a lack of material from critical areas. In addition, Tortonese doubted the validity of *Sphyrna oceanica* (1950a, p. 28), which, as he correctly suspected, is identical with *lewini*.

Fraser-Brunner (1950, pp. 213–219) synonymized *S. diplana* with *S. lewini*, although he continued to recognize *S. oceanica* as valid, citing supposed differences in size of eye, length of snout, relative position of first dorsal fin, size of second dorsal fin, and shape of head. Examination of specimens from the Gulf of Aden (BMNH 1925.7.20. 32.37), which were identified by Fraser-Brunner as *S. oceanica*, fails to substantiate his conclusion that this nominal species is a valid form.

DIAGNOSIS.—Characters mentioned in the diagnosis of the subgenus *Sphyrna* are not repeated here.

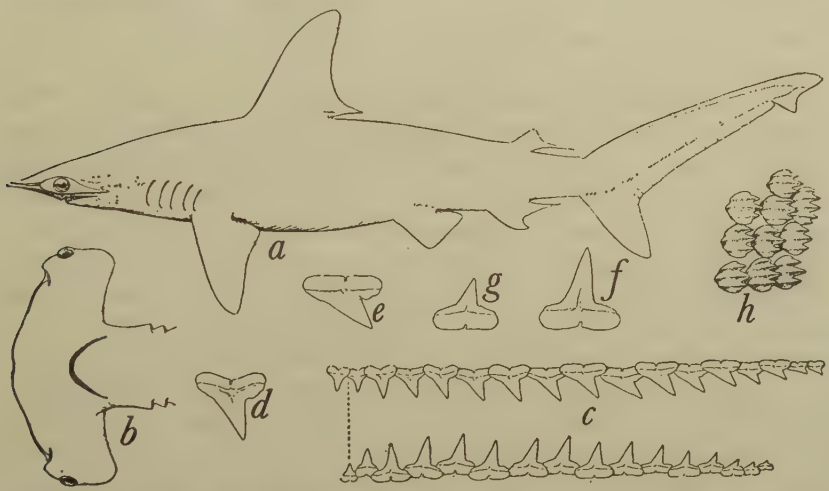


FIGURE 10.—*Sphyrna lewini: a*, juvenile female, 639 mm. TL, from Rio de Janeiro, Brazil (MCZ 462); *b*, ventral view of head; *c*, upper and lower teeth, left side, about 0.55 ×; *d*, fourth upper tooth; *e*, twelfth upper tooth; *f*, third lower tooth; *g*, eleventh lower tooth; *h*, dermal denticles, about 42 ×. (*d-g*, about natural size.) (From Bigelow and Schroeder, 1948, p. 415.)

Sphyrna lewini is characterized (as is *S. zygaena*, its closest relative) by a long second dorsal fin lobe and a low second dorsal fin, the length of the former about twice greatest height of fin. The anterior-median pore patch on the underside of the head is unique, the patch characterized by a rather sharp, smoothly rounded angle at the outer-posterior corner and by a narrow triangular area, which is devoid of pores, in the median-posterior region (fig. 22*d*).

S. lewini is distinguished from *S. zygaena* by a median indentation (scallop) on anterior margin of head; a shorter inner narial groove, which extends 40 to 45 percent of distance from inner margin of nares to tip of snout; orbit farther from nares, being separated by a distance slightly less than greatest horizontal diameter of eye; tip of second dorsal lobe reaching closer to upper precaudal pit, the lobe extending from three-fourths to four-fifths of distance from second dorsal base

to pit; a slightly less deeply falcate anal fin, the deepest part of the notch on the distal margin situated slightly anterior to a line drawn perpendicularly from the posterior axil of the fin; a longer anal base, the length of which is about equal to length of pectoral base; a more obtusely pointed posterior ridge to the upper precaudal pit (fig. 21*d*); occasional presence of a lower precaudal pit; presence of a rostral fenestra; and several chondrocranial characters (pl. 6B).

A comparison of *Sphyrna lewini* with other members of the genus is presented in table 1.

DESCRIPTION.—Meristic data appear in table 5. Characters mentioned in the diagnoses of the subgenus *Sphyrna* and of *S. lewini* are not repeated here.

Head moderately expanded, the greatest width from 24.0 to 30.2 percent of TL (in specimens less than 1,000 mm. long); shallow scallops present on anterior margin of head, about halfway between nares and tip of snout; outer posterior corner of lateral expansion of head posterior to corner of mouth, probably in specimens of all sizes; narial flap broad, moderately pointed at tip, with the outer edge curving evenly inward; orbit large, the horizontal diameter almost equal to length of shortest (fifth) gill slit; length of snout about one-third of head width in smaller specimens, to about one-fifth of head width in larger specimens; greatest transverse distance between corners of mouth from one-fifth to one-fourth of greatest width of head; symphysis of jaws situated posterior to a transverse line drawn between posterior margins of orbits in specimens of all sizes; labial furrow present at corner of lower jaw only (concealed when mouth is closed), about one-fifth to one-fourth as long as greatest horizontal diameter of eye.

Origin of first dorsal fin above or slightly posterior to axil of pectoral fin, a perpendicular line drawn ventrally from origin intersecting anterior third of pectoral fin; first dorsal fin broad, rather erect (not as erect as in large specimens of *Sphyrna tudes*), a line drawn perpendicularly from apex of fin passing close behind base; base of first dorsal fin about one-half length of head and from half again to almost twice length of pectoral fin base; anterior margin of first dorsal fin evenly curved, with part nearest apex very strongly curved; distal margin of first dorsal fin strongly falcate; lobe of first dorsal fin about one-third length of base; origin of second dorsal fin situated about halfway back above base of anal fin; second dorsal fin base from three-fifths to four-fifths length of anal fin base; anterior margin of pectoral fin from one-half to two-thirds length of head (higher values usually apply to larger individuals) and about equal to greatest vertical height of first dorsal fin; pectoral fin about two-thirds as broad as long; anterior margin of pectoral fin moderately convex; distal margin of pectoral

straight or slightly falcate; apex and inner corner of pectoral fin rounded; pelvic fin equal in length or slightly less (about four-fifths as long) than anal fin; pelvic fin base approximately equal in length to anal fin base; anterior margin of pelvic fin weakly convex, the distal margin nearly straight; anal fin equal in length or slightly greater than pelvic fin; height of anal fin about a third again as much as height of second dorsal fin; caudal fin nearly a third of TL; upper margin of caudal fin nearly straight; terminal part of caudal about one-fifth of total length of fin; posterior margin of terminal part of caudal fin moderately falcate; terminal apex of caudal narrowly rounded; lower lobe of caudal relatively narrow and long, the distance from angle included by upper and lower caudal lobes to tip of latter going from 1½ to 2 times in anterior margin of lower caudal lobe; lower caudal lobe one-third to two-fifths as long as upper lobe; lower caudal lobe fairly erect, sloping posteriorly at about a 35° angle from a perpendicular to body axis; anterior margin of lower caudal lobe weakly convex; posterior margin of lower lobe nearly straight.

Anterior margin of rostral node of chondrocranium nearly straight, or with a very shallow median indentation; accessory rostral cartilages absent; anterior fontanelle (viewed ventrally) appearing broad and shallowly U-shaped, with no noticeable median notch; prominent, bluntly rounded wings present on sides of rostral node; anterior wing of olfactory cartilage prominent, pointed, and projecting medially; anterior part of preorbital process long and slender, with a sharp angle on anterior edge; posterior part of preorbital process terminating in an evenly rounded knob.

Total number of vertebrae 174 to 204 (in nine specimens examined; only one individual with less than 192); body vertebrae 86 to 100, the relative number of body to caudal vertebrae varying from six more to twelve less.

Teeth $\frac{15 \text{ or } 16\text{–}0 \text{ to } 2\text{–}15 \text{ or } 16}{15 \text{ or } 16\text{–}1 \text{ or } 2\text{–}15 \text{ or } 16}$; teeth sometimes weakly serrate in large individuals; first tooth smaller than second, the 15th and 16th very small; teeth 1 through 3 in upper jaw nearly symmetrical and erect, with the subsequent teeth becoming increasingly oblique toward corners of mouth; cusps present on all teeth; lower teeth with somewhat narrower cusps than uppers, similarly oblique, but with successive series tending to become more erect and their cusps relatively more narrow with growth.

Dermal denticles (examined from upper part of back beneath first dorsal fin) closely overlapping, the blades thin and moderately arched; length of denticle (measured to tip of median marginal "tooth") as great, or nearly as great, as width; small specimens usually with three,

large specimens with four or five, sharp-toothed ridges, and as many pointed marginal teeth present on denticle; median tooth on denticle slightly longer than more distal teeth; pedicel very short, moderately slender.

Individuals deep olive to brownish-gray dorsally, shading to white ventrally; tip of ventral surface of pectoral fin faintly gray-black to dark black in life.

Maximum total length probably between 12 and 13 feet.

VARIATION.—With the possible exception of the teeth, *Sphyrna lewini* shows little noticeable geographic variation in external morphological characters. This can be seen from table 5, in which morphometric data have been recorded from specimens from throughout the range. Those characters that are considered to be of basic taxonomic importance, such as the structure of the chondrocranium (pl. 6B), the form of the anterior-median pore patch on the underside of the head (fig. 22*d*), the length and development of the intranarial groove, the position and length of the gill slits, and the shape and position of the fins, remain quite constant.

Although the teeth in *Sphyrna lewini* are ordinarily smooth, in some cases they may be very weakly serrate. This apparently occurs only in larger specimens, at least 5 or 6 feet in length. The serrated condition has long been thought to be characteristic only of the Pacific population (Sadowsky, 1965, p. 2), and, in fact, was one of the reasons for Springer's naming the Atlantic population as a new species, *S. diplana*. However, Dr. Shelton P. Applegate has recently informed me (in litt.) that he has seen specimens of this species from the western Atlantic with serrated teeth. In view of this, and because there seem to be no concomitant characters to suggest that more than one species is involved, I choose to regard *S. diplana* as a synonym of *S. lewini*.

A series of nine vertebral counts is available for specimens from widely scattered parts of the range. Although the total number of vertebrae ranges from 174 to 204, variation in eight of the nine individuals is only from 192 to 204. The reduced count in the other specimen (USNM 25180—from Charleston, S.C.) is due both to a decreased number of body and caudal vertebrae. It is difficult to say at this time what the significance of this unusually low count is.

RANGE—*Sphyrna lewini* is circumtropical in distribution (map 3). In the western Atlantic it occurs from southern Brazil (and possibly Uruguay) north to New Jersey (Bigelow and Schroeder, 1948, p. 419; Backus, 1960, p. 244). In the eastern Atlantic its range is not so well defined. It occurs in the Mediterranean Sea (Bigelow and Schroeder, 1948, p. 419) and along the African coast south at least to Liberia and Ghana (Bigelow and Schroeder, 1948, p. 419). The northern

limits of its range in the eastern Atlantic are uncertain, although it has never been recorded from the British Isles.

Sphyrna lewini is found in the western Pacific from southern Australia north to southern Japan and Korea, and in the eastern Pacific from northwestern South America to the Gulf of California. The fact that it is the only species of hammerhead definitely recorded from the Hawaiian Islands (Gosline and Brock, 1960, p. 91) may indicate that it is a more pelagic species than *Sphyrna mokarran*, which also logically might be expected to occur there.

MAP 3.—Distribution of *Sphyrna lewini*.
(The most westerly record from Africa is now known to represent *S. couardi;* solid=specimens examined; hollow=confirmed literature references.)

Sphyrna lewini apparently does not extensively penetrate cool waters (i.e., in which the temperature does not rise above the low 70's F.). Although its range overlaps that of *S. zygaena* to some extent, there are relatively few records of the two species having been taken together (Herald, 1961, p. 31, fig.).

Sphyrna (*Sphyrna*) *couardi* Cadenat

PLATES 9A, 10A

Sphyrna couardi Cadenat, 1951, pp. 98–99. (Original description; compared with *S. diplana* and *S. bigelowi;* tips of pectoral fins described as white; type locality: "off West Africa".)

Specimens examined.—Guinea: USNM uncataloged (1 head, 425 mm. in width), 12°06′ N, 17°22′ W.

DISCUSSION—*Sphyrna couardi* was described by Cadenat (1951, pp. 98–99) from "off West Africa." The description was very brief and there was no illustration, although the form was said to resemble *S. diplana* (=*S. lewini*), differing from that species (and from all other members of the family Sphyrnidae) in having the inferior part of the pectoral fin white and a longer and smaller head. While I have not seen a whole specimen of *S. couardi*, I have examined a large head (USNM uncatalogued) collected by Dr. Bruce B. Collette from off West Africa. This head, which is 425 mm. wide, has been compared with the head of a typical specimen of *S. lewini*, 445 mm. wide (USNM

uncataloged), from the same geographic area. Photographs of these appear in plate 10 and radiographs in plate 9.

The most striking difference between the two heads is the deeper, more robust appearance of *S. couardi* (also see measurements in table 10). This is confusing, since Cadenat described *S. couardi* as having a "longer and smaller" head than *S. lewini;* however, this apparent discrepancy may simply be a matter of semantics. The overall appearance of the head, in fact, seems closer to *S. mokarran* than *S. lewini;* however, *couardi* and *mokarran* may readily be distinguished by the presence of a distinct intranarial groove and nonserrated teeth in the former species, and by chondrocranial structure and differences in pore patterns on the ventral surface of the head.

The mucal pore patches on the ventral surface of the head are basically similar in *S. couardi* and *S. lewini,* although the anterior-median patch in the former is completely separated medially instead of being divided about halfway as in the latter (fig. 22*d*). The chondrocrania of the two forms also are similar (pls. 9 A, B), the main difference being in the appearance of the preorbital process. In *S. couardi* this structure is shorter and has a distinct knob at the angle, whereas in *S. lewini* it is longer and lacks a distinct knob. In addition, the olfactory wings in *S. couardi* are blunt and do not come to a sharp point as in *S. lewini.* In this case, however, the wing tips are rather ragged in appearance, suggesting that this possibly may be an aberrant condition.

In conclusion, the above evidence seems to indicate that *Sphyrna couardi* is a valid species of restricted range and that it is most closely related to *Sphyrna lewini.*

Subgenus *Platysqualus* Swainson

The subgenus *Platysqualus,* which is here considered to include *Sphyrna tudes, S. media, S. corona,* and *S. tiburo,* is distinguished by the following unique characters: First and fifth gill slits nearly equal in length and both somewhat shorter than the three middle slits; anal fin and anal fin base longer than in any other group of sphyrnids, the former 11.0 to 13.5 percent, and the latter 7.5 to 9.0 percent, of TL; anal base a fourth to half again as long as pectoral base; upper precaudal pit broadly semicircular or slightly pointed in shape, the ends pointing anteriorly (figs. 21*e-i*); lower precaudal pit present (this feature also sometimes present in *S. lewini*); fifth gill slit above insertion of pectoral fin (slightly posterior in *S. tiburo*); lobe of first dorsal fin extending past insertion of pelvic fin (in all but *S. tiburo*); teeth weak, nonserrated, with narrow pointed cusps; accessory rostral cartilages often present (none observed in *S. tiburo*).

In addition, the subgenus is characterized by: A fairly high second dorsal fin, its greatest height about equal to greatest height of anal fin; a shallowly falcate anal fin; eyes situated anterior to mouth, a line drawn between the posterior margins of orbits passing anterior to symphysis of jaws (intersecting symphysis in larger specimens of *S. tiburo*); a small orbit, separated from nares by a distance greater than horizontal diameter of orbit; absence of an outer narial groove; a variable total number of vertebrae, ranging in number from 142 to 202, with those over posterior part of coelomic cavity not enlarged; a small maximum size, probably not exceeding 4 or 5 feet. Perhaps the maximum size in some cases is even less (e.g., *S. corona*).

Sphyrna (Platysqualus) tiburo (Linnaeus)

DIAGNOSIS.—Characters mentioned in the diagnosis of the subgenus *Platysqualus* are not repeated here.

Sphyrna tiburo is unique among members of the genus *Sphyrna* in having the head only slightly expanded, either spade or shovel shaped, and measuring from 14.4 to 24.5 percent of TL in specimens up to 1,000 mm. long (higher values usually apply to smaller individuals and/or to individuals of the subspecies *vespertina*). The anterior-median pore patch on the underside of the head is also unique, the patch characterized by a rather sharp, but smoothly rounded angle at the posterior corner and by a long, narrow median posterior extension (fig. 22*e*).

Sphyrna tiburo is also distinguished by the anterior margin of the head being more or less evenly rounded between the eyes, with neither a median scallop nor narial depressions present; no inner narial groove; origin of first dorsal fin distinctly posterior to axil of pectoral fin, a perpendicular line drawn ventrally from origin of dorsal intersecting posterior part of pectoral fin; teeth not serrated, with short, weak, rather blunt cusps.

A comparison of *Sphyrna tiburo* with other members of the genus is presented in table 1.

DESCRIPTION.—Meristic data appear in table 6. Characters mentioned in the diagnoses of the subgenus *Platysqualus* and of *S. tiburo* are not repeated here.

Intranarial distance from one-tenth to one-sixth of TL (lower values usually apply to larger individuals); outer posterior corners of lateral expansions of head broadly rounded and situated posterior to corners of mouth; narial flap broad, blunt at tip, with the outer edge curving gradually inward; length of snout about two-fifths of head width; greatest transverse distance between corners of mouth from one-third to a little more than two-fifths of greatest width of head; symphysis of jaws situated, in smaller individuals, slightly

anterior to a transverse line drawn between posterior margins of orbits, while in larger individuals a line drawn between these points passes through the symphysis; a weakly marked labial furrow present on lower jaw only, the furrow extending only a short distance (concealed when mouth is closed).

Fourth gill slit situated anterior to, and fifth gill slit slightly posterior to, insertion of pectoral fin; posterior lobe of first dorsal fin terminating just anterior to insertion of pelvic fin (the dorsal and pelvic fins being in closer proximity only in *S. tudes*, *S. corona*, and *S. media*); first dorsal fin relatively slender, not perfectly erect, a line drawn perpendicularly from apex of fin barely intersecting lobe of fin; base of first dorsal fin about two-fifths length of head and at least half again length of pectoral fin base; anterior margin of first dorsal fin evenly curved, with the part nearest the apex more strongly curved; distal margin of first dorsal fin moderately falcate; lobe of first dorsal fin from four-ninths to almost one-half length of first dorsal base; origin of second dorsal fin situated about a third of way back above base of anal fin; second dorsal fin rather tall, its greatest height about two-thirds length of base, and about equal to greatest height of anal fin; second dorsal fin base about five-eighths of anal fin base; lobe of second dorsal fin rather long, its length about a third again greatest height of same fin, and extending about two-thirds of distance from posterior part of second dorsal base to upper precaudal pit; anterior margin of pectoral fin from one-half to nearly two-thirds length of head (higher values usually apply to larger individuals); pectoral fin four-fifths as broad as long; pectoral fin base five-eighths to three-fourths length of anal fin base; anterior margin of pectoral moderately convex; distal margin of pectoral nearly straight; apex and inner corner of pectoral rounded; pelvic fin about three-fourths length of anal fin; pelvic fin base about three-fourths length of anal fin base; anterior margin of pelvic fin weakly convex; distal margin of pelvic fin very shallowly falcate; anal fin about one-fourth again as long as pelvic fin; anal fin base from one-fourth to over one-third again as long as pectoral and pelvic fin bases, and from three-fifths again to nearly twice as long as second dorsal fin base; height of anal fin about equal to greatest height of second dorsal fin; anal fin weakly falcate toward apex and nearly straight toward tip of lobe; caudal fin from one-fourth to nearly one-third of total body length; upper margin of caudal nearly straight; terminal part of caudal about one-fourth of total length of fin; posterior margin of terminal part of caudal fin nearly straight or slightly falcate; both terminal and lower apices of caudal narrowly rounded in smaller specimens, somewhat more pointed in larger individuals; lower caudal lobe appearing relatively broad and short, the distance

from the angle included by the upper and lower caudal lobes to tip of latter going from 2 to 2½ times in anterior margin of lower caudal lobe; lower lobe of caudal one-third to two-fifths as long as upper lobe; lower caudal lobe sloping posteriorly at about a 45° angle from a perpendicular to the body axis; anterior margin of lower caudal lobe weakly convex; posterior margin of lower caudal lobe nearly straight.

Anterior margin of rostral node of chondrocranium either straight or with a poorly defined indentation; accessory rostral cartilages absent; rostral fenestra absent; anterior fontanelle (viewed ventrally) appearing broad and shallowly U-shaped, with a distinct, rounded, median notch; prominent pointed wings present on sides of rostral node; anterior wing of olfactory cartilage prominent, pointed, and projecting medially; anterior part of preorbital process short and rather blunt, with a moderately sharp angle on anterior edge; posterior part of preorbital process terminating in a knob, the anterior corner of which is evenly rounded and projects forward, and the posterior corner of which is somewhat more angulate (pls. 7 A, B).

Total number of vertebrae 142 to 172 (seven specimens examined); body vertebrae 71 to 88, the relative number of body to caudal vertebrae varying from 9 more to 2 less.

Teeth $\frac{12 \text{ to } 14\text{–}0 \text{ or } 1\text{–}12 \text{ to } 14}{12 \text{ to } 14\text{–}1\text{–}12 \text{ to } 14}$; teeth not serrate; first upper tooth erect and symmetrical, but subsequent upper teeth becoming increasingly oblique toward corners of mouth; teeth 3 through 10 or 11 largest in both jaws; cusps evident only on teeth 1 through 9 in specimens examined (through 11 or 12 according to Bigelow and Schroeder, 1948, p. 423); lower teeth shorter than upper teeth, with narrower cusps and slightly broader bases, the first through third teeth erect and symmetrical, the fourth through seventh or eighth slightly oblique, the eighth and subsequent teeth without cusps or definite cutting edges; three series of teeth functional in front and one or two series functional along side of upper jaw; four to six series functional in front, usually two functional along side, and three functional toward corner of mouth of lower jaw.

Dermal denticles (examined from upper part of back beneath first dorsal fin) closely overlapping, the blades rather steeply raised; length of denticle (measured to tip of median marginal "tooth") as great, or nearly as great, as width; five strong ridges usually present, and as many long, sharp-pointed teeth (these teeth are sometimes blunted or broken) usually present at posterior margin of denticle, the outer ridges and teeth sometimes rudimentary or absent, particularly in smaller individuals; median tooth on denticle ordinarily slightly longer than more distal teeth; pedicel short and slender.

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Individuals gray or grayish brown dorsally, becoming progressively more pale below, and often with small dark spots on side of body; occasional spots on caudal fin.

VARIATION.—Specimens of *Sphyrna tiburo* from the Pacific usually have more pointed heads than specimens from the Atlantic (figs. 12*a*, *b*). This difference is also reflected in proportional measurements, the relative width of the head and transverse distance between the nares averaging slightly greater for specimens from the Pacific (table 6 and fig. 13). As a result, Springer (1940a, pp. 161, 162) described the Pacific population as a new species, *Sphyrna vespertina*, although Bigelow and Schroeder (1948, p. 428) later placed it in the synonymy of *S. tiburo*.

For several reasons the two populations are regarded here as having differentiated only to the subspecies level. First, no differences comparable to those found for head shape were discovered for other morphometric characters (table 6). In addition, some individuals are intermediate in head shape (fig. 12*c*). As mentioned previously, such specimens possibly may have resulted from a partial reamalgamation of the populations following initial differentiation of the two forms.

Vertebral counts were made on four specimens of *S. tiburo tiburo* and three of *S. tiburo vespertina*. These counts, which range from 163 to 172 for the latter form and from 142 to 170 for the former, are interesting both because of the wide range in variation found in the typical subspecies and also because of the close agreement in vertebral number between two of the individuals of *S. tiburo tiburo* and the three specimens of *S. tiburo vespertina*. The two specimens of *S. tiburo tiburo* with the lowest counts (142 and 143) are from the eastern Gulf of Mexico, while those with the higher counts (159 and 170) are from Rhode Island and Brazil. (It should be mentioned here that these differences are not attributable solely to variation in number of caudal vertebrae.) Although it is possible that larger series of counts will show this apparent difference to be clinal in nature, a study of vertebral variation in sharks, recently completed by Drs. V. G. Springer and J. A. F. Garrick (1964) indicates the existence of a number of closely related species differing only in vertebral counts. This suggests that those specimens of *S. tiburo tiburo* from the eastern Gulf of Mexico represent a sibling form that may be distinguished from other populations of the same subspecies only by number of vertebrae.

RANGE.—Despite statements to the contrary (Bigelow and Schroeder, 1948, pp. 424–425; Herre, 1953, p. 27; Briggs, 1960, p. 173; and 1961, p. 552), there appear to be no substantiated records of *Sphyrna tiburo* outside of the Western Hemisphere.

Sphyrna tiburo tiburo is common in shallow, inshore waters of the western Atlantic, where it ranges from southern Brazil northward,

regularly, to southern North Carolina and, occasionally, to southern New England. All but three records are from continental waters, and these exceptions are from Bimini, in the western Bahamas, and from Cuba, less than 100 miles from the mainland. Although the species is known to be well established on Bimini, there is no evidence of a permanent population on Cuba, and it is possible that records from the latter area have resulted from market specimens that were caught on the other side of the Florida Straits.

Sphyrna tiburo vespertina is common in similar habitats in the eastern Pacific from southern California to Equador.

Locality records for *Sphyrna tiburo* are plotted on map 4.

***Sphyrna (Platysqualus) tiburo tiburo* (Linnaeus)**

FIGURES 11, 12*b*, *c*, 13, 21*e*, 22*e*; PLATE 7A

Squalus tiburo Linnaeus, 1758, p. 234. (Original description; no type specimen; type locality, "America".)

Sphyrna tiburo Rafinesque, 1810, p. 47. (New generic name for *Squalus tiburo* Linnaeus, 1758; misspelled "liburo," obviously a typographical error.)

Cestrorhinus tiburo Blainville, 1816, p. 121. (Name only.)

Zygaena tiburo Valenciennes, 1822, pp. 226–227. (Description; illustration of head; Brazil.)

Zygaena (*Squalus*) *tiburo* Leuckart, 1836, p. 22. (Illustration; early embryo, yolk stalk and yolk.)

Platysqualus tiburo Swainson, 1839, p. 318. (Description; new generic name proposed without comment.)

Sphyrnias tiburo Gray, 1851, p. 50. (In list.)

Reniceps tiburo Gill, 1861, pp. 403, 412. (Name; new generic name proposed despite availability of *Platysqualus*.)

Cestracion tiburo Gill 1862, p. 59. (In North American catalogue.)

Sphyrna (*Reniceps*) *tiburo* Jordan and Evermann, 1896, p. 217. (Range.)

Cestracion zygaena (misidentification) Radcliffe, 1916, pl. 43, fig. 2. (Photo of jaws, evidently mislabeled by accident.)

SPECIMENS EXAMINED.—(Range in size: 350–910 mm. TL). Bahamas: UMMZ 174384 (1), Bimini. Brazil: MCZ 464 (3), USNM 43359 (head and tail), Bahia; MCZ 469 (1), SU 52715 (1), SU 52873 (1), USNM 104318 (2), Recife (Pernambuco); SU 52713 (1), SU 52714 (1), Ponta de Mucuripe, Fortaleza; MCZ 27 (1), MCZ 90 (2), MCZ 153 (5), MCZ 162 (5), MCZ 394 (4), MCZ 416 (4), MCZ 439 (2), MCZ 450 (2), MCZ 461 (5), Rio de Janeiro; SU 14047 (1), FMNH 46997 (1), Santos; SU 52872 (1), Vitoria market. Colombia: USNM 94754 (1), Caribbean Sea, near Puerto Colombia (and Barranquilla). Cuba: USNM 2710 (1), MCZ 522 (2), no further data. Mexico: MCZ 39645 (1), off Ciudad Carmen, Campeche. Nicaragua: USNM 78180 (1), Punta Gorda. Panama: USNM 79315 (1), ANSP 49841–49847 (7), ANSP 49938–49940 (3 heads), Colon. Surinam: USNM 159198 (1), 06°27′ to 06°25′ N., 55°05′ to 55°10′ W.; USNM 159201 (1), 06°20′ to 06°19′ N., 54°33.5′ to 54°38.5′ W. United States

(Alabama): USNM 119827 (1), near Cedar Pt., Mississippi Sound. (Florida): USNM 26582 (1), UF 1407 (4), UF 5649 (1), UF 7061 (1), UF 8948 (1), Cedar Key, Levy Co.; USNM 30687 (1), Pensacola; USNM 34733–34734 (2), St. Marys River; USNM 39882 (1), off Cape Sable; USNM 47334 (1), USNM 184870 (1), Tampa Bay; USNM 57242 (1), Alligator Light; USNM 62773 (1), USNM 118995 (1), FMNH 7038 (1), Key West; USNM 92594 (1), USNM 116888 (1), MCZ 755 (1), Tortugas; USNM 108455 (1), SU 14329 (1), Englewood; USNM 125763 (1), near West Pass, Apalachicola Bay; CAS 19306 (1), MCZ 35847 (1), Pine Island Sound; UF 1416 (1), Daytona Beach pier,

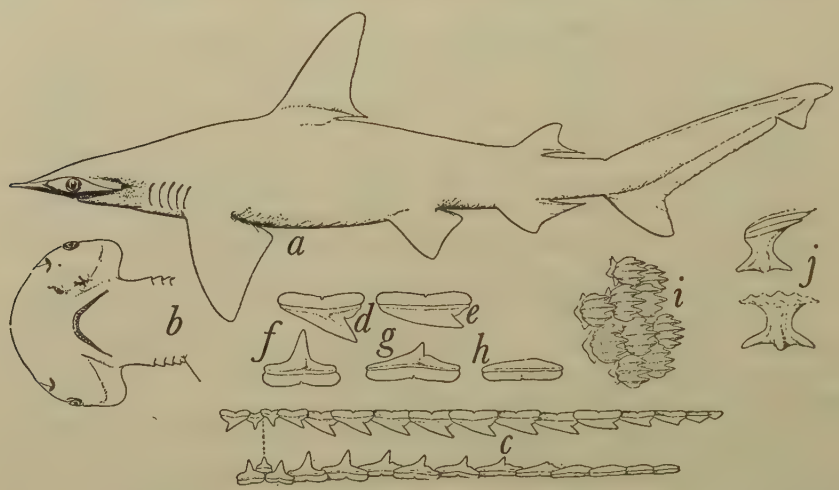


FIGURE 11.—*Sphyrna tiburo: a*, juvenile female, 367 mm. TL, from Rio de Janeiro, Brazil (MCZ 90); *b*, head of same specimen, ventral view; *c*, upper and lower teeth, left side, of male, 812 mm. TL, from Tortugas, Fla. (MCZ 848), about 1.5 ×; *d*, fourth upper tooth; *e*, tenth upper tooth; *f*, second lower tooth; *g*, seventh lower tooth; *h*, tenth lower tooth; *i*, dermal denticles, about 14 × (MCZ 90); *j*, lateral and apical views of dermal denticle, about 26 ×. (*d-h*, about 3 ×.) (From Bigelow and Schroeder, 1948, p. 421.)

Volusia Co.; UF 4208 (1), Fernandina Beach, Nassau Co.; UF 4211 (1), St. Augustine, St. Johns Co.; UF 7061 (1), Spanish Harbor Key (west end–Atlantic side), Monroe Co. (Georgia): UF 5463 (1), off St. Simons Island, Glynn Co. (Louisiana): USNM 127114–127115 (2), Barataria Bay channel; USNM 127116 (1), Bayou Fifi; USNM 155648 (1), Gulf of Mexico, south of New Orleans, 28°36′ N., 91°00′ W. (Mississippi): USNM 147793 (1), no further data; FMNH 21590 (1), Horn Island. (New Jersey): USNM 9270 (1), Delaware Bay, Beesleys Pt., between Great Egg and Peck Bays. (North Carolina): USNM 51894 (3), Beaufort. (Rhode Island): ANSP 581 (1), Newport. (South Carolina): USNM 25171 (1), MCZ 78 (skin), Charles-

ton. (Texas): USNM 82710 (2), Chame Point Pass; USNM 116450 (5), MCZ 35824–35825 (2), MCZ 36157 (1), MCZ 36240–36245 (9), Galveston; USNM 127101 (1), USNM 155964 (18), Corpus Christi; USNM 127104 (1), Harbor Island; USNM 127106 (1), Parateria (Grand Pass); USNM 127109 (1), ca. 13 mi. off Bay Chalaud; FMNH 37794–37796 (3), Port Aransas, Aransas; FMNH 11195–11198 (4), Laguna Madre, Point Isabel. (Virginia): USNM 125760 (1), Lynnhaven Roads, just west of Cape Henry light; MCZ 138 (skin), Hampton Roads; FMNH 1622 (1), Ocean View.

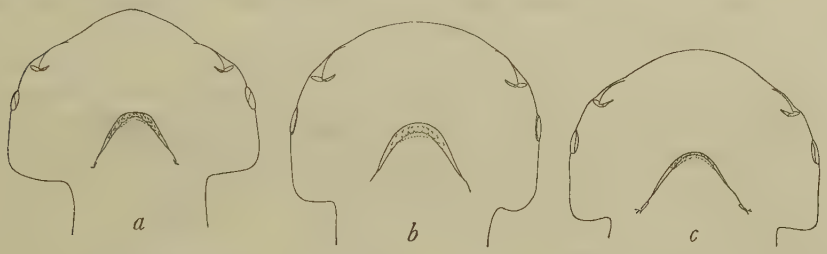


FIGURE 12.—*Sphyrna tiburo: a*, head of *S. t. vespertina*, a specimen 636 mm. TL (UCLA 58–46), from Gulf of California, showing pointed head; *b*, head of *S. t. tiburo*, a specimen 637 mm. TL (USNM 57242), from southern Florida, showing rounded head; *c*, head of *S. t. tiburo*, a specimen 880 mm. TL (USNM 127106), from Texas, showing intermediate condition of head. (Drawings by Dorothea B. Schultz.)

DIAGNOSIS.—*Sphyrna tiburo tiburo* differs from *S. tiburo vespertina* in having a slightly narrower and more evenly rounded head. These differences are illustrated in figures 12 and 13.

***Sphyrna (Platysqualus) tiburo vespertina* Springer**

FIGURE 12*a*; PLATE 7B

Sphyrna vespertina Springer, 1940a, pp. 161, 164–166. (Original description; comparisons; range; holotype, a 769 mm. female, SU 11584; type locality, Panama City; paratypes, a 520 mm. female, SU 11881, same locality as holotype; and a 938 mm. male, formerly Carnegie Museum no. 5675, from Guayaquil, Ecuador.)

SPECIMENS EXAMINED.—(Range in size: 277–880 mm. TL). Ecuador: USNM 88677 (1), FMNH 59350 (1), Guayaquil. El Salvador: USNM 21627 (1), Acajutla. Mexico: USNM 190595 (1), Camorore Beach, ca. 3 mi. north of Mazatlán, Sinaloa; UCLA 51–4 (1), Gulf of California, Bocochibampo Bay, Sonora; UCLA 52–250 (4), Almejas Bay, at anchorage off Santa Margarita Island, Baja California; UCLA 58–46 (1), Gulf of California, south of Bahia Topolobampo, off Isla San Ignacio and Isla Macapule, Sinaloa; CAS (W 55–167) (1), Gulf of California, south end of Angel de la Guarda Island; CAS 3987 (1), Guaymas; SIO 47–53 (1), Gulf of California, 15

mi. from mouth of Río Colorado, Baja California. Panama: USNM 190591 (2), Panama Bay, 1–3 mi. SE of Isla Taboga and 2–4 mi. from Rio Pacora; UCLA 53–275 (3), Panama Bay, between Panama City and Punta Gorda; UCLA 58–305 (1), Panama Bay, offshore between Rio Chico and Punta de la Plata; FMNH 62438 (2), Punta Chame and Punta Anton, Panama Bay; SU 11584 (holotype of *Sphyrna vespertina*), Panama City; SU 11881 (one paratype of *S. vespertina*), Panama City; MCZ 80 (1), MCZ 516 (1), no further data.

Diagnosis.—*Sphyrna tiburo vespertina* differs from *S. tiburo tiburo* in having a slightly broader and more pointed head. These differences are illustrated in figures 12 and 13.

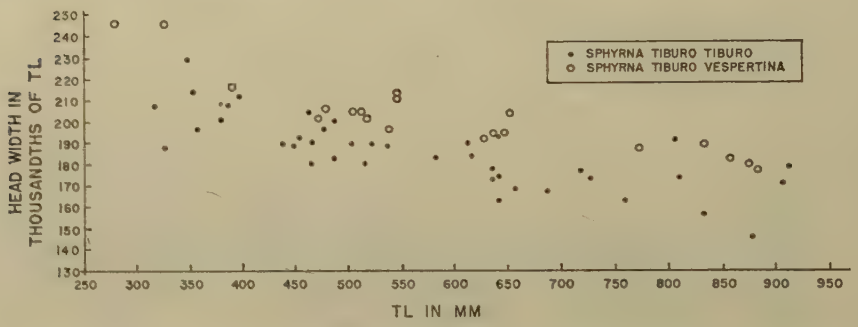


Figure 13.—Comparison of head width in the two subspecies of *Sphyrna tiburo*. (Figure by Paul Laessle.)

Sphyrna (*Platysqualus*) *media* Springer

Figures 14, 15, 16, 17, 21 *f*, *g*, 22*f*; Plate 7c

Sphyrna tudes (misidentification) Jordan, 1895, p. 383. (Mazatlán, Sinaloa.)

Cestracion tudes (misidentification) Meek and Hildebrand, 1923, p. 59. (Colón, Panama.)

?*Sphyrna tiburo* (misidentification) Kumada and Hiyama, 1937, p. 17. (Description could apply to either *S. tiburo*, *S. media*, or *S. corona*; illustration is either of *S. media* or *S. corona*.)

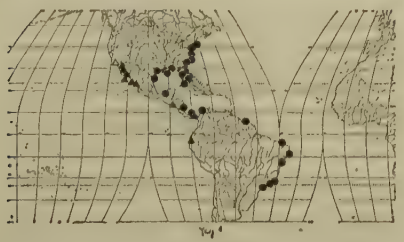
Sphyrna media Springer, 1940a, pp. 161–169. (Original description; illustration of head; holotype, a partially deflesbed 900 mm. male, SU 11583; type locality, Mazatlán, Sinaloa, Mexico; one paratype, a 745 mm. female, USNM 28160, from Mazatlán.)

Sphyrna nana Sadowsky, 1965, pp. 1–12. (Original description; illustrations of head and body; holotype, a 1,330 mm. female, São Paulo Zoological Museum [POB] 7172; type locality, off Cananéia, Brazil [lat. 25° S., long. 47°52′ W.].)

Specimens examined.—(Range in size: 337–900 mm. TL; heads of larger specimens also examined; estimated length of largest, ca. 1025 mm.). Atlantic Ocean (including Caribbean Sea): Brazil: SU 52716 (head only), Vitoria. Panama: MCZ 500 (1), USNM 79284 (1), Colon market.

Pacific Ocean: Costa Rica: USNM 196140 (6), Gulf of Nicoya. Mexico: UCLA 58–47 (2, including one head), Gulf of California, south of Bahia Topolobampo, off Isla San Ignacio and Isla Macapule, Sinaloa; FMNH 63093 (2), above San Benito, Chiapas; SIO 60–88 (3), Gulf of California, 21°55′ N., 105°37′ W.; SU 11583 (holotype of *Sphyrna media*—partial skin), Mazatlan, Sinaloa; USNM 28160 (1 paratype of *Sphyrna media*), Mazatlan, Sinaloa. Panama: USNM 190593 (4), UCLA 58–304 (4, including three heads), (all originally UCLA 58–304), Panama Bay, offshore between Punta de Hicacal and Rio Pasiga; USNM 50376 (1), no further data.

Initially *Sphyrna media* and *Sphyrna corona* were regarded by me as synonymous. This conclusion was based mainly on the fact that difference in anterior contour of the head, which was the primary basis for Springer's original separation of the two forms, does not remain constant, the head shape grading from the more evenly rounded condition of *S. media* to the more lobate situation found in *S. corona*. In addition, the chondrocrania of the two forms are very similar, as are



MAP 4.—Distribution of subspecies.
● *Sphyrna tiburo tiburo*
▲ *Sphyrna tiburo vespertina*
(Solid=specimens examined; hollow=confirmed literature references.)

the various external morphological features. Closer examination of the chondrocrania, however, revealed several relatively small, but nonetheless constant, differences. With a firm basis for separation thus available, it was found that other morphological differences, which were at first thought to be due to individual variation, also could be used to separate the two species. The various distinguishing features are discussed in the diagnoses of the respective species.

DIAGNOSIS.—Characters mentioned in the diagnosis of the subgenus *Platysqualus* are not repeated here.

Sphyrna media differs from the closely related *S. tudes* in the following characters: Anterior margin of head more rounded (particularly in large specimens), with no pronounced median notch; inner narial groove absent; anterior-median pore patch on underside of head with the posterior margin more broadly rounded than in *S. tudes* and with a pointed median-posterior extension (fig. 22*f*); narial depression very shallow; first dorsal fin of larger specimens (600 mm. or more) less erect and less broadly triangular, a line drawn perpendicularly from apex of fin not intersecting base of fin.

Sphyrna media differs from *S. corona* in having a narrower postorbital process to the chondrocranium, with the anterior edge of this structure posterior, rather than anterior, to the angle formed by the juncture of the innerorbital and anterior mediorbital cartilages (pl.7c); a slightly deeper anterior fontanelle; and shorter rostral cartilages. The last difference has been objectively shown by dividing the transverse distance between the tips of the preorbital cartilages into the

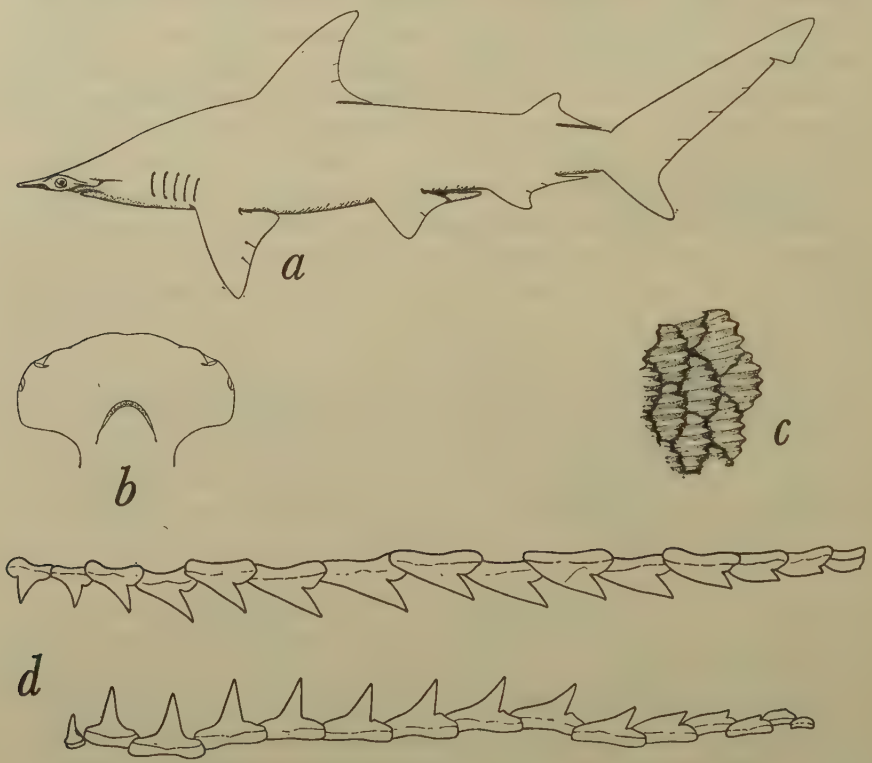


FIGURE 14.—*Sphyrna media: a*, adult male, 900 mm. TL, from Panama Bay (UCLA 58–304); *b*, head of same specimen, about 0.12 ×; *c*, dermal denticles of same specimen; *d*, upper and lower teeth, left side, of same specimen, about 1.5 ×. (Drawings by Dorothea B. Schultz.)

length of the rostral cartilage. For *S. media* the range of values thus obtained is from 18.1 to 24.0 percent, and for *S. corona* from 25.9 to 30.5 percent; these have been plotted and may be seen in figure 17.

Sphyrna media also differs from *S. corona* in having a slightly shorter snout. A comparison of snout lengths may be seen in figures 15*b*, 16, and 18*b*. Although there is some overlap in values for the two species, when specimens of a comparable size are compared lower values are obtained for *S. media*.

Sphyrna media also differs from *S. corona* in having: The anal fin more deeply falcate and with a more pointed apex (figs. 14*a*, 15*a*); anterior-median pore patch on underside of head with the posterior margin more broadly rounded and with a pointed median-posterior extension (fig. 22*f*); a more pointed upper precaudal pit in smaller specimens (fig. 21*g*); and a slightly wider mouth. When the transverse distance between the corners of the mouth is divided by the head width, the values obtained are somewhat greater for *S. media* Finally, *Sphyrna media* may be a larger species. The largest specimen of *Sphyrna media* seen (a head) was calculated to be 1025 mm. TL, while of the 17 specimens of *Sphyrna corona* examined, the largest (the holotype) measured only 672 mm. More specimens of *S. corona* must be seen to definitely confirm this, however.

A comparison of *Sphyrna media* with other members of the genus is presented in table 1.

DESCRIPTION.—Meristic data appear in table 7. Characters mentioned in the diagnoses of the subgenus *Platysqualus* and of *S. media* are not repeated here.

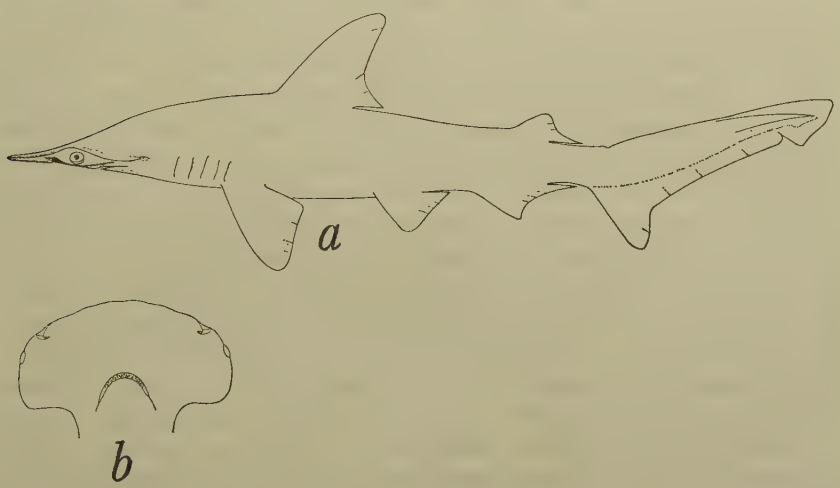


FIGURE 15.—*Sphyrna media: a*, juvenile female, 356 mm. TL, from Chiapas, Mexico (FMNH 63093); *b*, head of same specimen. (Drawings by Paul Laessle.)

Head moderately expanded, the greatest width measuring from 22.3 to 27.3 percent of TL; character of anterior-median margin of head somewhat variable, evenly rounded in some individuals, with no median indentation, and with a broad, very shallow median depression in others; outer posterior corner of lateral expansion of head situated anterior to corner of mouth; narial flap broad, bluntly pointed at tip, with the broadly curved outer edge curving sharply inward; a

very short labial furrow present at corner of lower jaw in larger specimens, not noticeable in smaller specimens.

Origin of first dorsal fin slightly posterior to axil of pectoral fin, a perpendicular line drawn ventrally from origin intersecting anterior third of pectoral fin; base of first dorsal fin one-third to one-half length of head and about twice length of pectoral fin base; anterior margin of first dorsal fin broadly and evenly curved, particularly in larger individuals; distal margin of first dorsal fin rather deeply falcate, particularly on lower two-thirds of fin; lobe of first dorsal fin from two-fifths to one-half length of first dorsal base; origin of second dorsal fin situated about two-fifths of way back above base of anal fin; second dorsal fin tall, its greatest height about three-fourths length of base and from three-fourths to four-fifths of greatest height of anal fin; second dorsal fin base from one-half to five-eighths of anal fin base; lobe of second dorsal fin rather long, its length about a third again greatest height of fin and extending from two-thirds to three-fourths of distance from posterior part of second dorsal base to upper precaudal pit; pectoral fin from two-fifths to two-thirds length of head (higher values usually apply to larger individuals); pectoral fin two-thirds as broad as long; length of pectoral fin base from five-eighths to three-fourths length of anal fin base; inner two-thirds of anterior margin of pectoral fin straight, outer third slightly convex; distal margin of pectoral fin slightly falcate; apex of pectoral broadly pointed in small specimens, slightly more acute in larger individuals; inner corner of pectoral narrowly rounded; length of pelvic fin from two-thirds to four-fifths length of anal fin; length of pelvic fin base from five-ninths to three-fourths length of anal fin base; anterior margin of pelvic fin straight or slightly convex; distal margin of pelvic very slightly falcate; anal fin from one-tenth to one-third again as long as pelvic fin; length of anal fin base one-fourth to four-ninths again as long as pectoral and pelvic fin bases and from three-fifths again to nearly twice as long as second dorsal fin base; height of anal fin one-fifth to one-fourth greater than height of second dorsal fin; length of caudal fin from one-fourth to nearly one-third of total body length; upper margin of caudal fin evenly convex; terminal part of caudal slightly less than one-fourth of total length of fin; lower posterior margin of terminal part of caudal fin nearly straight or slightly falcate; both terminal and lower apices of caudal broadly pointed; lower lobe of caudal appearing relatively narrow and long, particularly in larger individuals, the distance from the angle included by the upper and lower caudal lobes to tip of latter going about 1¾ times in anterior margin of lower caudal lobe; lower caudal lobe about one-third as long as upper lobe; lower caudal lobe rather erect, sloping posteriorly at about a 25 to 30° angle from a

perpendicular to the body axis; anterior margin of lower caudal lobe weakly convex toward base, more strongly convex toward apex; posterior margin of lower caudal lobe nearly straight.

Anterior margin of rostral node of chondrocranium varying slightly, from broadly convex to broadly and shallowly concave; rostral fenestra absent; anterior fontanelle (viewed dorsally) deep and broadly U-shaped, with the sides of the U slanting slightly inward; a distinct median notch present on anterior fontanelle; fairly prominent (though not as prominent as in *S. tudes*), broad, obtusely pointed wings present

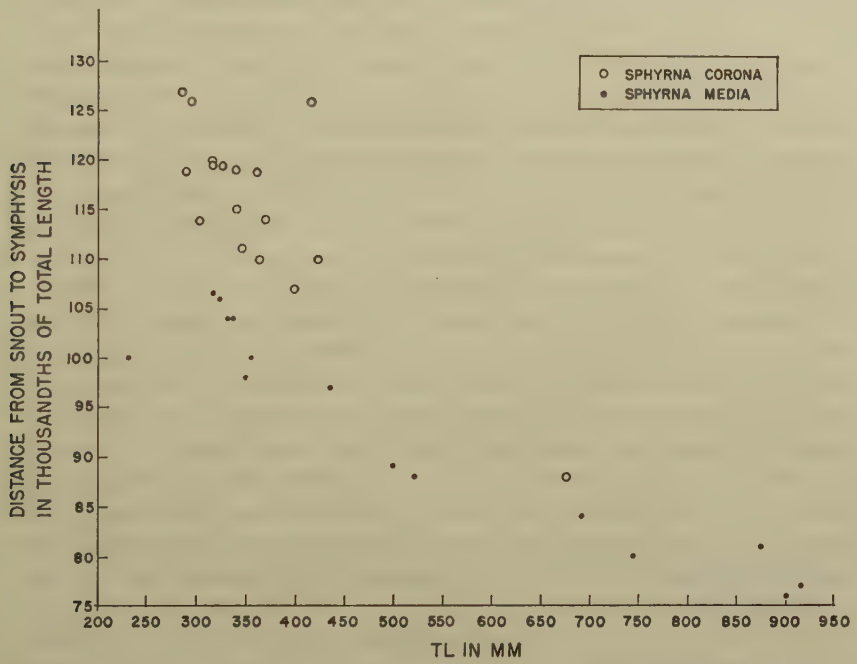


FIGURE 16.—Comparison of snout length in *Sphyrna media* and *Sphyrna corona*. (Figure by Paul Laessle.)

on sides of rostral node; anterior wing of olfactory cartilage fairly prominent (though not as prominent as in *S. tudes*), pointed, and projecting medially; tip of anterior part of preorbital process short (not as short as in *S. mokarran*) and rather thick, with a sharp angle on the anterior edge.

Total number of vertebrae 191 to 196 (10 specimens examined); body vertebrae 100 to 103, there being from 7 to 14 more body than caudal vertebrae.

Teeth $\frac{14\text{–}1\text{–}13}{14\text{–}1\text{–}14}$, $\frac{14\text{–}1\text{–}14}{14\text{–}1\text{–}14}$, $\frac{14\text{–}0\text{–}14}{13\text{–}1\text{–}14}$, $\frac{13\text{–}2\text{–}12}{14\text{–}1\text{–}14}$, $\frac{13\text{–}2\text{–}13}{14\text{–}1\text{–}14}$, and $\frac{13\text{–}1\text{–}12}{13\text{–}1\text{–}13}$

(first two counts listed by Springer, [1940a, p. 163]); upper teeth oblique, becoming increasingly so toward corners of mouth in upper jaw; teeth 6 to 9 or 10 longest, the outer teeth very low, but with a definite cusp; in lower jaw, teeth 2 through 8 longest (tooth 1 not markedly smaller however), the outermost two or three teeth very short, round, and without a definite cusp; one or two series of teeth functional in alternating rows along sides of upper jaw and two to three rows along sides of lower jaw.

Dermal denticles (examined from upper part of back beneath first dorsal fin) evenly and closely spaced, overlapping but little, the blades thick and rather strongly arched; length of denticle (measured to tip of median marginal "tooth") less than width; small specimens with three, larger specimens usually with up to five, sharp-topped ridges, and as many sharp-pointed marginal teeth (especially deep and pointed in small individuals) on denticle; median tooth on denticle slightly longer than more distal teeth; pedicel short and broad.

Individuals gray or grayish brown dorsally, becoming progressively more pale below; no markings on fins.

Status of *Sphyrna nana*.—Sadowsky (1965) recently described a new species of hammerhead, *Sphyrna nana*, from southern Brazil, based on a single adult female, 1,330 millimeters long. This form was said to differ from *S. media* in having a shorter snout, a larger orbit, the anterior margin of the head not regularly oval and with prenarial convexities, a shorter distance between the eye and nares, a shorter distance between the nares, a shorter upper caudal lobe, a greater interdorsal distance, and a longer first dorsal fin base. Unfortunately, no mention was made either of the morphology of the chondrocranium or of the arrangement of the mucal pores on the ventral surface of the head.

The following measurements were given for the holotype of *S. nana:* Head width (190); snout to first gill slit (169); snout to first dorsal origin (308); snout to second dorsal origin (637); distance between first and second dorsal bases (233); snout to pectoral insertion (204); snout to pelvic insertion (466); horizontal diameter of orbit (15); length of first dorsal base (95); length of second dorsal base (43); length of second dorsal lobe (45); height of second dorsal fin (37); length of anal base (80); length of anal lobe (33); height of anal fin (36); length of pectoral base (54); length of pelvic base (34); length of caudal fin (251). If one compares these measurements with those listed for *S. media* in table 7, it can be seen that, for those characters that undergo little or no proportional change with an increase in total body length, the values for *S. nana* generally fall within the range of values for *S. media*. For those characters that undergo pronounced

allometric change with an increase in length (head width, distance from snout to symphysis, head length, distance between first and second dorsal bases, and snout to pectoral insertion), the values given for *S. nana* are about what one would expect in individuals of *media* around 1,300 millimeters long. Of the various measurements listed for *S. nana*, only three (distance from snout to pelvic insertion, horizontal diameter of orbit, and length of caudal fin) seem to fall outside the range of variation one would normally expect to find in a large individual of *S. media*.

Thus, with few exceptions the proportional measurements in *S. nana* and *S. media* are very similar, and those in which there is slight disagreement are not sufficiently different to warrant recognition of a second species. The contour of the anterior margin of the head, another character that supposedly differentiates *S. nana* and *S. media*, falls within the normal range of variation for *S. media* (as discussed elsewhere in this paper).

In conclusion, while the validity of *S. nana* cannot be categorically denied until the natures of the chondrocranium and the pore patches on the ventral surface of the head are known, I so far can find no evidence to indicate that it is specifically distinct from *S. media*.

VARIATION.—*Sphyrna media* shows more than the usual amount of variation in configuration of the anterior margin of the head. Some specimens have an evenly rounded head (fig. 15*b*), while in others the head is faintly lobate, with a slight median indentation or scallop (fig. 14*b*). Those individuals with more lobate heads may be distinguished only with difficulty from specimens of *S. corona*. That this condition is not strictly a function of size is shown by the fact that one of the largest specimens of *S. media* examined, a 900 mm. male (UCLA 58–304) from Panama Bay, was at first identified as *S. corona* on the basis of head shape.

Variation in the median scallop on the anterior margin of the head was found to result from a comparable variation in the tip of the rostral cartilage. Considerable variation was found also in the degree of development and/or presence of the accessory rostral cartilages, a single series of specimens sometimes showing all degrees of development.

RANGE.—*Sphyrna media* occurs in the eastern Pacific, from the Gulf of California south at least as far as Panama Bay, in the southern Caribbean, and in the southwestern Atlantic (map 5).

The occurrence of *Sphyrna media* in the Caribbean is confirmed by two specimens (USNM 79284, MCZ 500) from the Colon (Panama) market, which were collected around the turn of the century. Presence of the species in this area is further substantiated by Stewart

Springer (1949, pp. 17–26), who lists (under the name "scoophead shark") a female, 1,125 mm. long, containing eight embryos, which was collected in April 1949, from the Gulf of Paria, Trinidad.

There is, in the Stanford University collection, the head of a specimen of this species (SU 52716) from Vitoria, Brazil. Since this locality is so far removed from Trinidad, the next closest place from which *S. media* has been recorded, one might regard the record with suspicion. However, the intervening area has not been well collected, and further exploration will likely show the species to be more widely distributed in the western Atlantic than presently appears.

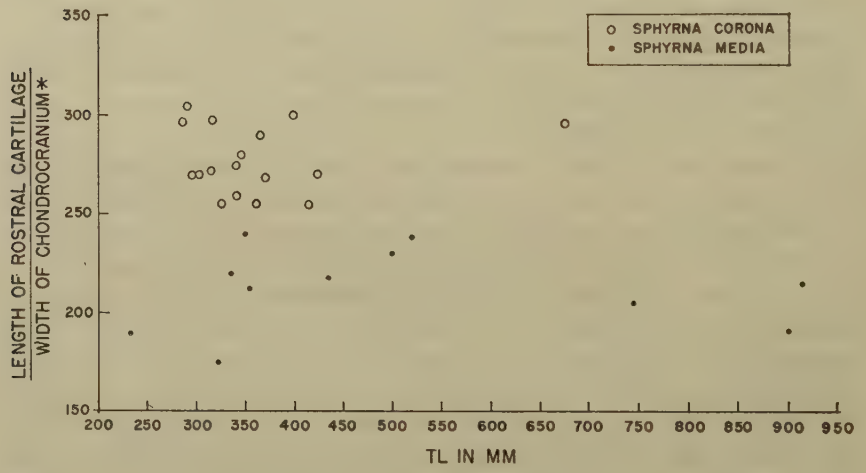


FIGURE 17.—Comparison of rostral cartilage length (expressed as a ratio) in *Sphyrna media* and *Sphyrna corona*. Width of chondrocranium measured from tips of preorbital cartilages. (Figure by Paul Laessle.)

Sphyrna (Platysqualus) corona Springer

FIGURES 16, 17, 18, 21*h*, 22*g*; PLATE 7D

?*Sphyrna tiburo* (misidentification) Kumada and Hiyama, 1937, p. 17. (Description could apply to either *S. tiburo* or *S. media;* illustration is either of *S. media* or *S. corona*.)

Sphyrna corona Springer, 1940a, pp. 161–169. (Original description; illustration of head; holotype, a 672 mm. male, SU 11882; type locality, Panama Bay, at Panama City, Panama.)

SPECIMENS EXAMINED.—(Range in size: 231–672 mm. TL). Pacific Ocean: Colombia: UCLA 51–283 (1), Boca Candelaria, 50 mi. south of Buenaventura. Costa Rica: UCLA 54–167 (1), Golfo de Nicoya, Chira Flats, off Isla Chira. Mexico: FMNH 72521 (2), off Chiapas coast, above San Benito. Panama: CAS (W 53–273) (3), Panama Bay, 1–3 mi. southeast of Taboga, and 2–4 mi. off Rio Pacora; UCLA

53–275 (9), Panama Bay, between Panama City and Punta Gorda; SU 11882 (holotype of *Sphyrna corona*), Panama City.

DIAGNOSIS.—Characters mentioned in the diagnosis of the subgenus *Platysqualus* are not repeated here.

Sphyrna corona differs from the closely related *S. tudes* in much the same way that *S. media* differs from that species (see diagnosis of *S. media*). Unlike *S. media*, however, the shape of the anterior-median pore patch on the underside of the head is very similar in *S. corona* and *S. tudes* (figs. 22*g*,*h*).

Sphyrna corona differs from *S. media* in having a broader postorbital process to the chondrocranium, with the anterior edge of this structure anterior, rather than posterior, to the angle formed by the juncture

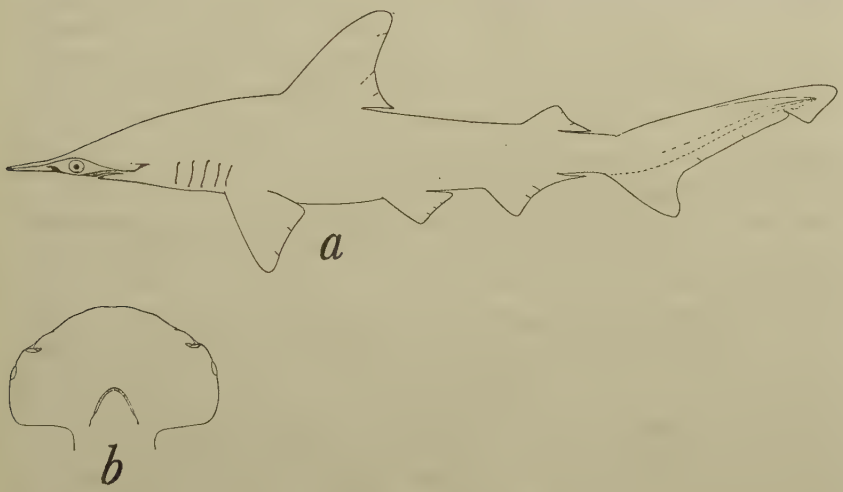


FIGURE 18.—*Sphyrna corona: a*, juvenile female, 371 mm. TL, from Chiapas, Mexico (FMNH 72521, ex 63093); *b*, head of juvenile male, 402 mm. TL, from Panama Bay (UCLA 53–275), about 0.6 × natural size. (Fig. *a* drawn by Paul Laessle, fig. *b* by Dorothea B. Schultz.)

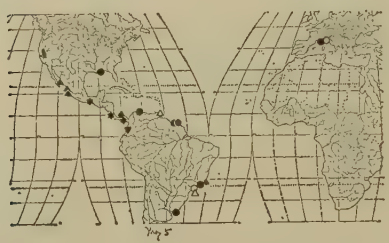
of the innerorbital and anterior mediorbital cartilages (pls. 7C,D); a slightly shallower anterior fontanelle; and longer rostral cartilages. (The last character is discussed at greater length in the diagnosis of *S. media*.)

Sphyrna corona also differs from *S. media* in having: A slightly longer snout (fig. 18*b*); a less deeply falcate anal fin with a more rounded apex (fig. 18*a*); anterior-median pore patch on underside of head with the posterior margin less broadly rounded and without a pointed median-posterior extension (fig. 22*g*); a more broadly rounded upper precaudal pit in smaller specimens (fig. 21*h*); and a slightly narrower mouth. Finally, *S. corona* may not reach as large a max-

imum size as *S. media*, because the largest specimen examined (672 mm.) was little over half as large as the largest specimen of *S. media* that was seen.

A comparison of *Sphyrna corona* with other members of the genus is presented in table 1.

DESCRIPTION.—Since most of the morphological characters in *Sphyrna corona* are similar to those found in *S. media*, the following description has been condensed so as to avoid repetition. Only those



MAP 5.—Distribution of species.
● *Sphyrna tudes* ▲ *Sphyrna media*
▼ *Sphyrna corona*
★ *Sphyrna media* and *Sphyrna corona*
(Solid = specimens examined; hollow = confirmed literature references.)

characters in which actual counts or measurements are cited are listed in the following account. For other characters see either the diagnoses of *S. corona* or the subgenus *Platysqualus*, or the description of *S. media*.

Meristic data appear in table 8.

Head moderately expanded, the greatest width measuring from 23.7 to 29.1 percent of TL; teeth $\frac{13–?–13}{12–1–13}$ (count given for holotype by Springer, 1940a, p. 163) $\frac{14–14}{14–1–14}$ and $\frac{14–14}{14–1–14}$.

RANGE.—*Sphyrna corona* has one of the most restricted ranges of any species of hammerhead, occurring only in the eastern Pacific from southern Mexico south at least to the coast of Colombia (map 5).

Sphyrna (*Platysqualus*) *tudes* (Valenciennes)

FIGURES 19, 20, 21*i*, 22*h*; PLATES 4, 8

Zygaena tudes Valenciennes, 1822, pp. 225–226. (Illustration of head; original description [apparently based on two species, *S. tudes* and *S. mokarran*]; types from Nice and Cayenne are *S. tudes*, as here recognized, while type from Coromandel probably is *S. mokarran*.)

Sphyrna tudes Müller and Henle, 1841, p. 53. (In part; identification by reference to Valenciennes, 1822.)

Sphyrna bigelowi Springer, 1944, pp. 274–276. (Original description; illustration; type locality, Uruguay; holotype, a 385 mm. male [USNM 87682]; paratypes, a 395 mm. male from Uruguay [USNM 120751], and a 900 mm. female from Rio de Janeiro, Brazil [MCZ 463].)

SPECIMENS EXAMINED.—(Range in size: 213–900 mm. TL). Western Atlantic Ocean (including Caribbean Sea and Gulf of Mexico):

Brazil: MCZ 463 (paratype of *S. bigelowi*), Rio de Janeiro. French Guiana: MNHN 1019 (lectoparatype of *Zygaena tudes*), Cayenne. Surinam: ANSP 377 (1), ANSP 516 (1), (no further data); USNM 156721 (1), 1 mi. southeast of Paramaraibo light ship; USNM 159197 (1), USNM 159199 (1), 06°27′ to 06°25′N., 55°05′ to 55°10′W.; USNM 159227 (2), 06°20.5′N. to 06°19.5′N., 54°54′W. to 54°49′W.; USNM 159228 (4), USNM 159229 (4), 06°22′N., 55°04′ to 55°08′W. United States (Mississippi): USNM 195957 (8), Gulf of Mexico, 29°54′N., 88°06′W. (Oregon Sta. 2110). Uruguay: USNM 87682 (holotype of *Sphyrna bigelowi*), no further data; USNM 120751 (paratype of *S. bigelowi*), no further data. Venezuela: USNM 123217 (head), Gulf of Venezuela, Anway Bay.

Mediterranean Sea: France: MNHN 1049 (lectotype of *Zygaena tudes*), Nice.

NOMENCLATURE.—The original description of *Zygaena tudes* (Valenciennes, 1822, pp. 225–226, pl. 12, figs. 1*a* and *b*) was based on specimens, in the Museum National d'Histoire Naturelle, from Nice, France (cat. no 1049); Cayenne, French Guiana (cat. no. 1019); and Coromandel, India (specimen lost). As has previously been shown, these specimens comprise two species: The one currently called *Sphyrna tudes* (Gilbert, 1961, p. 480), which is characterized by the tip of the first dorsal fin extending beyond the insertion of the pelvic fins, the first and fifth gill slits nearly equal in length, with the latter situated above the insertion of the pectoral fin, and a small maximum size (perhaps not over 4 or 5 feet); and the one presently called *Sphyrna mokarran* (Gilbert, 1961), characterized by the tip of the first dorsal fin not reaching the insertion of the pelvic fins, the first gill slit longer than the fifth gill slit, with the latter situated posterior to the insertion of the pectoral fin, and a large maximum size (up to 20 feet). I here restrict the name *tudes* to those specimens from Nice and Cayenne, and designate as lectotype of *Zygaena tudes* the 346 mm. female (no. 1049) on which the illustration in the original description was based (pl. 4).

DIAGNOSIS.—Characters mentioned in the diagnosis of the subgenus *Platysqualus* are not repeated here.

Sphyrna tudes differs from the closely related *S. corona* and *S. media* in the following characters: Anterior margin of head straighter (particularly in large specimens), with a pronounced median notch; inner narial groove present; anterior-median pore patch on underside of head divided into two broadly rounded lobes and separated by a deep, wide, median indentation (fig. 22*b*); narial depression slightly deeper; first dorsal fin of larger specimens (600 mm. or more) more erect and more broadly triangular, a line drawn perpendicularly from apex of fin intersecting base of fin.

A comparison of *Sphyrna tudes* with other members of the genus is presented in table 1.

DESCRIPTION.—Meristic data appear in table 9. Characters mentioned in the diagnoses of the subgenus *Platysqualus* and of *S. tudes* are not repeated here.

Head moderately expanded, the greatest width measuring from 27.5 to 31.5 percent of TL; inner narial groove extending 3.5 to 4.0 percent of distance from narial openings to median notch; outer posterior corner of lateral expansion of head situated posterior to

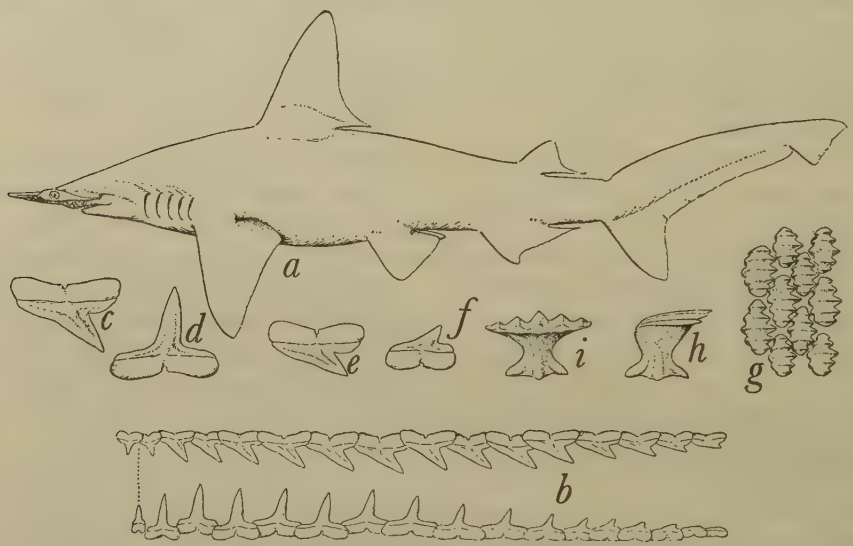


FIGURE 19.—*Sphyrna tudes: a*, subadult male, 886 mm. TL, from Rio de Janeiro, Brazil (MCZ 463); *b*, upper and lower teeth, left side, of same specimen, about 1.5 ×; *c*, fifth upper tooth; *d*, twelfth upper tooth; *e*, fifth lower tooth; *f*, twelfth lower tooth; *g*, dermal denticles of MCZ 463, about 17 ×; *h*, dermal denticle, side view, about 34 ×; *i*, dermal denticle, apical view, about 34 ×. (*c-f*, about 3 ×.) (From Bigelow and Schroeder, 1948, p. 410.)

corner of mouth in smaller specimens, anterior to corner of mouth in larger individuals; narial flap rather narrow (particularly in smaller specimens), pointed at tip, with the broadly curved outer edge curving sharply inward; length of snout about two-fifths of head width in smaller specimens to about one-third of head width in larger specimens; greatest transverse distance between corners of mouth from one-fifth to one-fourth of greatest width of head; a very short labial furrow present at corner of lower jaw in larger specimens, not noticeable in smaller specimens.

Origin of first dorsal fin slightly posterior to axil of pectoral fin, a perpendicular line drawn ventrally from origin intersecting anterior

third of pectoral fin; base of first dorsal fin three-eighths to four-ninths length of head and from a third again to not quite twice length of pectoral fin base; anterior margin of first dorsal fin broadly and evenly curved, particularly in larger individuals, with the part nearest the apex a little more strongly curved; upper distal margin of first dorsal broadly convex, lower margin broadly but distinctly falcate; lobe of first dorsal fin a little less than one-half length of first dorsal base; origin of second dorsal fin situated about two-fifths of way back above base of anal fin; second dorsal fin tall, its greatest height from two-thirds to four-fifths length of base and from two-thirds to four-

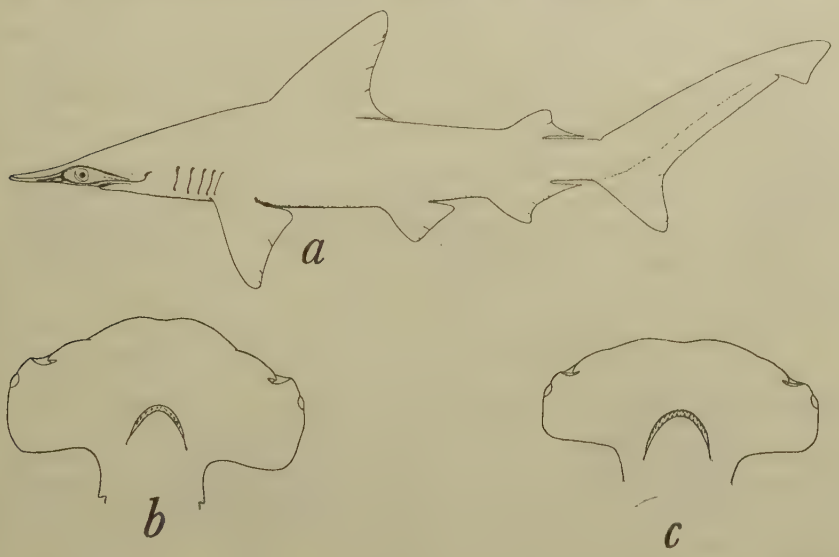


FIGURE 20.—*Sphyrna tudes: a*, juvenile female, 402 mm. TL, from Mississippi (USNM 195957); *b*, head of same specimen, about 0.3 ×; *c*, head of small adult, from Gulf of Venezuela (USNM 123217), about 0.18 ×. (Drawings by Dorothea B. Schultz.)

fifths of greatest height of anal fin; second dorsal fin base slightly greater than one-half of anal fin base; lobe of second dorsal fin long, its length from a third to half again greatest height of fin, and extending from two-thirds to three-fourths of distance from posterior part of second dorsal base to upper precaudal pit; pectoral fin from one-half to two-thirds length of head (higher values usually apply to larger individuals); pectoral fin two-thirds as broad as long; length of pectoral fin base from two-thirds to three-fourths length of anal fin base; inner two-thirds of anterior margin of pectoral fin straight, outer third distinctly convex; distal margin of pectoral fin nearly straight or very slightly falcate; apex of pectoral broadly pointed;

inner corner of pectoral fin narrowly rounded; length of pelvic fin from two-thirds to nine-tenths length of anal fin; length of pelvic fin base from five-ninths to seven-eighths length of anal fin base; anterior and distal margins of pelvic fin nearly straight; anal fin from one-eighth to one-third again as long as pelvic fin; length of anal fin base from one-third to one-half again as long as pectoral and pelvic fin bases and about twice as long as second dorsal fin base; height of

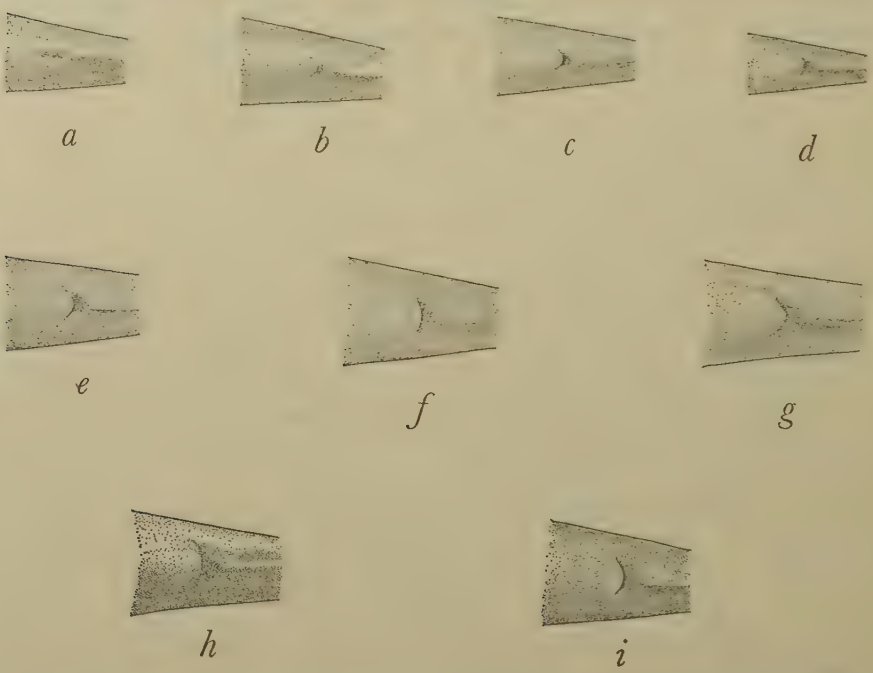


FIGURE 21.—Appearance of upper precaudal pit: *a*, *Sphyrna blochii*, 615 mm. female, from North Borneo (FMNH 21836); *b*, *S. mokarran*, 675 mm. male, from Florida (USNM 106543); *c*, *S. zygaena*, 580 mm. male, from Virginia (USNM 119699); *d*, *S. lewini*, 495 mm. female, from Texas; *e*, *S. t. tiburo*, 880 mm. female, from Texas (USNM 127106); *f*, *S. media*, 900 mm. female, from Panama Bay (UCLA 58–304); *g*, *S. media*, 356 mm. female, from Chiapas (FMNH 63093); *h*, *S. corona*, 371 mm. male, from Chiapas (FMNH 72521, ex. 63093); *i*, *S. tudes*, 825 mm. male, from Surinam (USNM 156721). (Figs. *a-f*, *i* drawn by Dorothea B. Schultz; figs. *g*, *h* by Paul Laessle.)

anal fin from one-fifth to one-third greater than height of second dorsal fin; anal fin deeply falcate toward apex, nearly straight toward tip of lobe; length of caudal fin nearly a third of total body length; upper margin of caudal fin slightly convex; terminal part of caudal about one-fourth of total length of fin; lower posterior margin of terminal part of caudal fin nearly straight or slightly falcate; both terminal and lower apices of caudal broadly pointed; lower lobe of

caudal appearing relatively narrow and long, the distance from the angle included by the upper and lower caudal lobes to tip of latter going about 1½ times in anterior margin of lower caudal lobe; lower caudal lobe about one-third as long as upper lobe; lower caudal lobe rather erect, sloping posteriorly at about a 25 to 30° angle from a perpendicular to the body axis; anterior margin of lower caudal lobe weakly convex; posterior margin of lower lobe nearly straight.

Anterior margin of rostral node of chondrocranium with a broad, deep, median indentation; accessory rostral cartilages usually present; rostral fenestra usually absent (present in one individual examined); anterior fontanelle (viewed dorsally) deep and broadly V-shaped, with an indistinct median notch on the posterior margin; prominent, broad, obtusely pointed wings present on sides of rostral node; anterior wing of olfactory cartilage prominent, pointed, and projecting medially; tip of preorbital process short (though not as short as in *S. mokarran*), rather thick, with a sharp angle on the anterior edge; postorbital process terminating in an angular knob, the anterior corner of which may be either broadly pointed or narrowly rounded, and the posterior corner of which forms a broadly rounded angle.

Total number of vertebrae numbering from 195 to 202 (five specimens examined); body vertebrae numbering from 107 to 110, there being from 12 to 25 more body than caudal vertebrae.

Teeth $\frac{15\text{–}0\text{–}15}{16\text{–}1\text{–}15}$ and $\frac{16\text{–}0\text{–}16}{15\text{–}1\text{–}15}$ (two specimens counted; latter count for lectotype); upper teeth oblique, becoming increasingly so toward corners of mouth in upper jaw; teeth 4 or 5 to 11 longest, the outer teeth very low, but with a definite cusp; in lower jaw teeth 2 to 7 or 8 longest, the outermost two very short, rounded, without a definite cusp; one or two series of teeth functional in alternating rows along sides of lower jaw, and two to three rows along sides of lower jaw.

Dermal denticles (examined from upper part of back beneath first dorsal fin) evenly and closely spaced, overlapping but little, the blades thick and rather strongly arched; length of denticle (measured to tip of median marginal "tooth") less than width; small specimens with three, larger specimens usually with up to five, sharp-topped ridges, and as many sharp-pointed marginal teeth (especially deep and pointed in small individuals) on denticle; median tooth on denticle slightly longer than more distal teeth; pedicel long and rather slender.

Individuals gray or grayish brown dorsally, becoming progressively more pale below; no markings on fins.

VARIATION.—Examination of the lectotype (designated elsewhere in this paper) of *Zygaena tudes*, a 346 mm. female from Nice, France, indicates that the Mediterranean and western Atlantic populations of *Sphyrna tudes* are morphologically indistinguishable. The only un-

usual feature of the lectotype is the presence of a small rostral fenestra (pl. 8B). However, the occasional presence of such a fenestra in *S. zygaena* and *S. blochii* (in which species it is ordinarily absent) suggests that the type specimen is merely a variant with regard to this character.

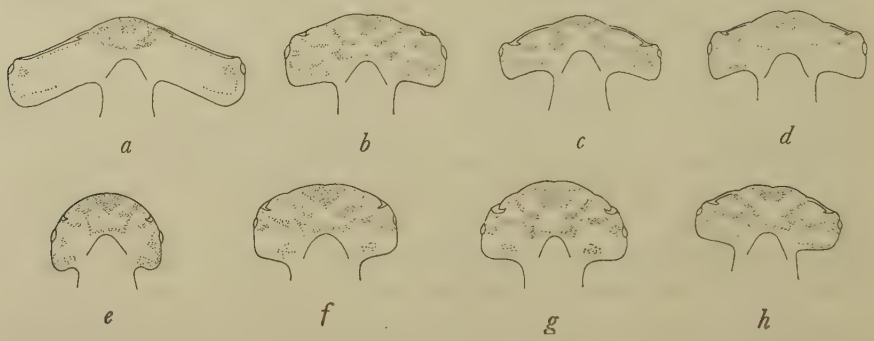


FIGURE 22.—Distribution of pores on ventral side of head: *a, Sphyrna blochii; b, S. mokarran; c, S. zygaena; d, S. lewini; e, S. tiburo; f, S. media; g, S. corona; h, S. tudes.* (Drawings by Paul Laessle.)

RANGE.—*Sphyrna tudes* is restricted to the western Atlantic Ocean and the western Mediterranean Sea. In the western Atlantic it occurs from Uruguay (Springer, 1944, p. 274) to the northern Gulf of Mexico (Gilbert, 1961, p. 480). In the western Mediterranean it is recorded from Nice, France (the type locality) and Livorno, Italy (Tortonese, 1950a, pp. 31, 32; 1950b, p. 1031).

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TABLE 1.—*Comparison of important diagnostic characters in species of* Sphyrna [1]

	Outer narial groove	Inner narial groove	Median indentation of snout	Size of orbit [2]	Length of anal base [3]	Width of head [4]	Position of 5th gill relative to pectoral fins	Position of 1st dorsal fin tip relative to pelvic fins	Distal margin of pelvic fin	Teeth	Lower precaudal pit	Rostral fenestra
S. blochii	Present	Present	Present	Small	Short	Very wide	Posterior	Anterior	Straight	Smooth	Absent	Absent [7]
S. mokarran	Absent	Absent	Present	Large	Short	Wide	Posterior	Anterior	Falcate	Serrate	Absent	Present
S. zygaena	Absent	Present	Absent	Large	Short	Wide	Posterior	Anterior	Straight	Smooth [5]	Absent	Absent [7]
S. lewini	Absent	Present	Present	Large	Short	Wide	Posterior	Anterior	Straight	Smooth [6]	Absent	Present
S. conardi	Absent	Present	Present	Large		Wide				Smooth		Present
S. tiburo	Absent	Absent	Absent	Intermediate	Long	Narrow	Above	Anterior	Straight	Smooth	Present	Absent
S. media	Absent	Absent	Present [8]	Small	Long	Wide	Above	Posterior	Straight	Smooth	Present	Absent
S. corona	Absent	Absent	Present [8]	Small	Long	Wide	Above	Posterior	Straight	Smooth	Present	Absent
S. tudes	Absent	Present	Present	Small	Long	Wide	Above	Posterior	Straight	Smooth	Present	Absent [7]

[1] Numerical values expressed in thousandths of total length; values are for specimens under 1000 mm. TL.
[2] Large: usually over 20; small: usually under 20.
[3] Long: usually over 65; short: usually under 65.
[4] Very wide: usually over 400; wide: usually 230–300; narrow: usually under 200.
[5] Weakly serrate in adults.
[6] Sometimes weakly serrate in adults.
[7] Small fenestra occasionally present.
[8] Poorly developed, often absent in *S. media*.

TABLE 2.—*Measurements of* Sphyrna blochii (*proportions expressed in thousandths of total length*)

	Size range in mm.			
	300–399	400–599	600–799	>800
	Number of specimens			
	4	4	2	1
Head width	337–492(391.2)	441–481(463.8)	432–456(444.0)	420
Internarial distance	152–165(157.5)	160–167(164.0)	153–164(158.5)	152
Snout to symphysis	66–78(70.8)	63–72(66.5)	56–64(60.0)	54
Head length	221–237(229.0)	197–213(205.0)	195–197(196.0)	195
Snout to 1st gill slit	173–176(174.5)	151–168(159.5)	153–154(153.5)	153
Snout to 1st dorsal origin	244–266(256.5)	217–258(228.8)	214–219(216.5)	214
Snout to 2nd dorsal origin	565–626(583.3)	560–575(565.8)	577–584(580.5)	567
Distance between 1st and 2nd dorsal bases.	191–248(216.5)	209–242(226.8)	243–247(245.0)	232
Snout to pectoral insertion	187–224(204.8)	193–206(197.5)	171–204(187.5)	191
Snout to pelvic insertion	392–432(415.3)	390–420(408.3)	395–397(396.0)	395
Horizontal diameter of orbit	14–21(16.5)	14–18(15.8)	13–15(14.0)	13
Length of 1st dorsal base	105–113(110.3)	103–114(107.8)	111–117(114.0)	121
Length of 2nd dorsal base	35–44(39.3)	34–40(37.5)	39–40(39.5)	44
Length of pectoral base	51–56(53.5)	50–58(53.5)	54–63(58.5)	55
Length of pelvic base	52–59(55.3)	53–54(53.5)	59–60(59.5)	61
Length of 2nd dorsal lobe	43–47(44.8)	47–53(50.0)	50–57(53.5)	51
Height of 2nd dorsal fin	22–30(26.0)	22–27(24.3)	26–27(26.5)	28
Length of anal base	58–62(60.0)	55–65(60.3)	69–71(70.0)	64
Length of anal lobe	34–39(36.3)	39–44(40.8)	38–45(41.5)	39
Height of anal fin	32–36(33.8)	34–39(37.0)	37–38(37.5)	40
Length of caudal fin	317–329(323.5)	332–339(335.8)	335–338(336.5)	331

TABLE 3.—*Measurements of* Sphyrna mokarran (*proportions expressed in thousandths of total length*)

	Size range in mm. (N=number of specimens)			
	N	400–599	N	600–799
Head width				
Atlantic	3	231–244(239.3)	1	235
Pacific	4	225–230(228.3)	1	273
Internarial distance				
Atlantic	3	170–175(173.0)	1	170
Pacific	4	157–173(164.8)	1	190
Snout to symphysis				
Atlantic	3	73–81(78.0)	1	73
Pacific	4	66–80(74.3)	1	82
Head length				
Atlantic	3	220–232(227.3)	1	226
Pacific	4	212–235(226.5)	1	250
Snout to 1st gill slit				
Atlantic	3	177–187(182.3)	1	171
Pacific	4	166–187(179.8)	1	200
Snout to 1st dorsal origin				
Atlantic	3	273–289(280.7)	1	284
Pacific	4	253–289(277.3)	1	285

TABLE 3.—*Measurements of* Sphyrna mokarran *(proportions expressed in thousandths of total length)*—Continued

	Size range in mm. (N=number of specimens)			
	N	400–599	N	600–799
Snout to 2nd dorsal origin				
Atlantic	3	581–600(592.3)	1	595
Pacific	4	555–579(568.5)	1	599
Distance between 1st and 2nd dorsal bases				
Atlantic	3	193–211(202.7)	1	213
Pacific	4	189–205(196.0)	1	208
Snout to pectoral insertion				
Atlantic	3	197–215(204.3)	1	207
Pacific	4	187–226(211.0)	1	244
Snout to pelvic insertion				
Atlantic	3	421–436(427.3)	1	434
Pacific	4	432–449(439.5)	1	469
Horizontal diameter of orbit				
Atlantic	3	20–25(22.7)	1	22
Pacific	4	29–33(31.3)	1	26
Length of 1st dorsal base				
Atlantic	3	97–100(99.0)	1	98
Pacific	4	85–98(92.7)	1	106
Length of 2nd dorsal base				
Atlantic	3	54–67(60.0)	1	52
Pacific	4	41–51(45.8)	1	56
Length of 2nd dorsal lobe				
Atlantic	3	40–46(42.3)	1	39
Pacific	4	46–48(46.5)	1	45
Height of 2nd dorsal fin				
Atlantic	3	28–39(33.3)	1	38
Pacific	4	27–41(35.3)	1	47
Length of anal base				
Atlantic	3	61–67(64.0)	1	61
Pacific	4	56–73(63.5)	1	67
Length of anal lobe				
Atlantic	3	33(33.0)	1	30
Pacific	4	32–39(35.3)	1	31
Height of anal fin				
Atlantic	3	28–33(30.0)	1	33
Pacific	4	34–40(36.5)	1	40
Length of pectoral base				
Atlantic	3	53–58(55.7)	1	54
Pacific	4	49–54(51.8)	1	58
Length of pelvic base				
Atlantic	3	56–59(57.3)	1	60
Pacific	4	53–56(54.8)	1	56
Length of caudal fin				
Atlantic	3	310–335(325.3)	1	309
Pacific	4	307–320(313.0)	1	289

TABLE 4.—*Measurements of* Sphyrna zygaena (*proportions expressed in thousandths of total length*)

	Size range in mm. (N=number of specimens)					
	N	400–599	N	600–799	N	>800
Head width						
Atlantic	8	261–290(276.9)	3	262–276(268.7)	0	—
Pacific	10	261–285(273.3)	2	276–279(277.5)	1	260
Internarial distance						
Atlantic	8	194–209(201.5)	3	189–198(193.3)	0	—
Pacific	10	190–207(197.3)	2	191–203(197.0)	1	186
Snout to symphysis						
Atlantic	8	62–77(70.6)	3	67–70(68.3)	0	—
Pacific	10	65–73(69.6)	2	64–65(64.5)	1	45
Head length						
Atlantic	8	219–245(230.8)	3	218–226(221.3)	0	—
Pacific	10	225–242(231.9)	2	219–227(223. 0)	1	210
Snout to 1st gill slit						
Atlantic	8	170–192(178.3)	3	168–180(173.3)	0	—
Pacific	10	172–189(180.4)	2	167–171(169.0)	1	162
Snout to 1st dorsal origin						
Atlantic	8	264–291(275.6)	3	267–270(269.0)	0	—
Pacific	10	266–288(278.5)	2	263–274(268.5)	1	273
Snout to 2nd dorsal origin						
Atlantic	8	589–626(606.4)	3	595–602(599.0)	0	—
Pacific	10	592–626(605.3)	2	602–614(608.0)	1	635
Distance between 1st and 2nd dorsal bases						
Atlantic	8	228–245(236.1)	3	238–251(243.0)	0	—
Pacific	10	221–244(236.1)	2	241–253(247.0)	1	—
Snout to pectoral insertion						
Atlantic	8	207–224(214.5)	3	198–207(203.3)	0	—
Pacific	10	209–226(217.1)	2	195–202(198.5)	1	198
Snout to pelvic insertion						
Atlantic	8	440–468(450.3)	3	438–446(443.3)	0	—
Pacific	10	440–458(451.3)	2	439–443(441.0)	1	454
Horizontal diameter of orbit						
Atlantic	8	23–30(25.8)	3	23–25(24.0)	0	—
Pacific	10	24–31(28.0)	2	24(24.0)	1	12
Length of 1st dorsal base						
Atlantic	8	90–105(95.8)	3	91–98(95.0)	0	—
Pacific	10	86–105(95.8)	2	93–100(96.5)	1	102
Length of 2nd dorsal base						
Atlantic	8	28–35(31.9)	3	30–33(31.3)	0	—
Pacific	10	29–38(33.3)	2	28–38(33.7)	1	25

TABLE 4.—*Measurements of* Sphyrna zygaena *(proportions expressed in thousandths of total length)*—Continued

	Size range in mm. (N=number of specimens)					
	N	400–599	N	600–799	N	>800
Length of 2nd dorsal lobe						
Atlantic	8	43–52(47.0)	3	44–47(45.7)	0	—
Pacific	10	43–48(45.1)	2	46–49(47.5)	1	—
Height of 2nd dorsal fin						
Atlantic	8	16–22(18.9)	3	18–21(19.7)	0	—
Pacific	10	16–23(19.5)	2	21–23(22.0)	1	—
Length of anal base						
Atlantic	8	43–57(47.3)	3	42–47(45.0)	0	—
Pacific	10	44–52(46.9)	2	42–44(43.0)	1	—
Length of anal lobe						
Atlantic	8	39–44(42.1)	3	42–44(43.3)	0	—
Pacific	10	38–43(41.1)	2	43–45(44.0)	1	—
Height of anal fin						
Atlantic	8	24–35(27.6)	3	26–29(27.7)	0	—
Pacific	10	24–30(27.0)	2	26–27(26.5)	1	29
Length of pectoral base						
Atlantic	8	47–58(53.4)	3	50–57(54.0)	0	—
Pacific	10	49–56(52.8)	2	53–60(56.5)	1	—
Length of pelvic base						
Atlantic	8	40–46(43.1)	3	39–45(42.0)	0	—
Pacific	10	41–47(44.3)	2	40–41(40.5)	1	—
Length of caudal fin						
Atlantic	8	293–311(303.5)	3	290–301(294.7)	0	—
Pacific	10	295–312(303.1)	2	298(298.0)	1	269

TABLE 5.—*Measurements of* Sphyrna lewini *(proportions expressed in thousandths of total length)*

	Size range in mm. (N=number of specimens)									
	N	300–399	N	400–599	N	600–799	N	800–900	N	>1,000
Head width										
Atlantic	2	280–284(282)	16	268–302(287.0)	6	258–285(274.0)	1	257	1	240
Eastern Pacific	—	—	8	260–291(276.1)	4	256–277(267.5)	—	—	—	—
Western Pacific and Indo-Australia	2	266–285(275.5)	12	246–287(264.8)	3	261–280(269.0)	—	—	—	—
Internarial distance										
Atlantic	2	205–213(209.0)	16	190–218(203.9)	6	193–212(201.7)	1	181	1	175
Eastern Pacific		—	8	187–211(200.3)	4	184–202(195.8)		—		—
Western Pacific and Indo-Australia	2	197–204(200.5)	12	180–214(193.3)	3	186–205(197.3)		—		—
Snout to symphysis										
Atlantic	2	81–86(83.5)	16	72–83(79.1)	6	67–77(71.3)	1	64	1	46
Eastern Pacific	—	—	8	73–81(77.8)	4	68–73(70.3)	—	—	—	—
Western Pacific and Indo-Australia	2	83–85(84)	12	69–83(73.9)	3	66–70(67.3)	—	—	1	41

TABLE 5.—*Measurements of* Sphyrna lewini (*proportions expressed in thousandths of total length*)—Continued

	Size range in mm. (N=number of specimens)									
	N	300–399	N	400–599	N	600–799	N	800–900	N	>1,000
Head length										
Atlantic	2	253–265(259.0)	16	220–256(241.0)	6	217–238(227.7)	1	210	1	197
Eastern Pacific	—	—	8	221–247(233.7)	4	216–237(225.0)	—	—	—	—
Western Pacific and Indo-Australia	2	244–273(258.5)	12	213–250(233.0)	3	203–226(215.3)	—	—		—
Snout to 1st gill slit										
Atlantic	2	198–200(199.0)	16	177–196(189.6)	6	166–192(177.3)	1	168	1	162
Eastern Pacific		—	8	174–200(188.6)	4	160–184(173.8)		—		—
Western Pacific and Indo-Australia	2	194–206(200.0)	12	169–196(181.8)	3	165–179(170.0)		—		—
Snout to 1st dorsal origin										
Atlantic	2	282–307(294.5)	16	261–298(285.7)	6	268–285(277.1)	1	259	1	230
Eastern Pacific	—	—	8	279–303(291.8)	4	263–286(273.4)	—	—	—	—
Western Pacific and Indo-Australia	2	294–301(297.5)	12	276–312(294.4)	3	254–271(263.7)	—	—	1	282
Snout to 2nd dorsal origin										
Atlantic	2	606–618(612.0)	16	587–625(603.4)	6	572–600(584.7)	1	575	1	551
Eastern Pacific	—	—	8	591–637(612.9)	4	579–606(591.3)	—	—	—	—
Western Pacific and Indo-Australia	2	593–622(607.5)	12	598–657(615.3)	3	591–602(595.0)	—	—	—	—
Between 1st and 2nd dorsal bases										
Atlantic	2	198–207(202.5)	16	199–224(210.0)	6	222–242(232.7)	1	233	1	227
Eastern Pacific	—	—	8	196–222(210.4)	4	208–240(228.5)	—	—	—	—
Western Pacific and Indo-Australia	2	195–219(207.0)	12	194–244(213.9)	3	219–236(226.0)	—	—	1	281
Snout to pectoral insertion										
Atlantic	2	230–235(232.5)	16	202–242(225.8)	6	199–221(211.8)	1	200	1	177
Eastern Pacific	—	—	8	216–233(222.3)	4	206–232(215.3)	—	—	—	—
Western Pacific and Indo-Australia	2	225–253(239.0)	12	200–231(217.2)	3	206–215(210.3)	—	—	1	196
Snout to pelvic insertion										
Atlantic	2	460–464(462.0)	16	435–472(450.1)	6	427–456(441.7)	1	422	1	390
Eastern Pacific	—	—	8	429–462(446.0)	4	431–459(442.0)	—	—	—	—
Western Pacific and Indo-Australia	2	456–479(467.5)	12	404–475(444.3)	3	439–451(445.3)	—	—	1	464
Horizontal diameter of orbit										
Atlantic	2	26(26)	16	21–29(23.8)	6	19–22(20.8)	1	19	1	14
Eastern Pacific	—	—	8	21–26(23.5)	4	21–23(21.8)	—	—	—	—
Western Pacific and Indo-Australia	2	27–28(27.5)	12	20–26(23.4)	3	21(21)	—	—	1	11
Length of 1st dorsal base										
Atlantic	2	105–111(108.0)	16	93–113(107.7)	6	94–106(101.0)	1	95	1	94
Eastern Pacific	—	—	8	99–110(104.2)	4	92–102(98.5)	—	—	—	—
Western Pacific and Indo-Australia	2	97–109(103.0)	12	92–110(104.3)	3	102–110(106.3)	—	—	1	91
Length of 2nd dorsal base										
Atlantic	2	35–37(36.0)	16	34–42(38.6)	6	32–40(36.3)	1	35	1	35
Eastern Pacific	—	—	8	32–41(36.4)	4	31–38(34.8)	—	—	—	—
Western Pacific and Indo-Australia	2	34–38(36.0)	12	28–38(34.0)	3	33–44(37.0)	—	—	1	23

TABLE 5.—*Measurements of* Sphyrna lewini (*proportions expressed in thousandths of total length*)—Continued

	Size range in mm. (N=number of specimens)									
	N	300–399	N	400–599	N	600–799	N	800–900	N	>1,000
Length of 2nd dorsal lobe										
Atlantic	2	49–50(49.5)	16	43–53(49.0)	6	44–51(48.2)	1	48	1	48
Eastern Pacific	—	—	8	45–52(48.9)	4	47–50(48.5)	—	—	—	—
Western Pacific and Indo-Australia	2	45–51(48.0)	12	44–56(49.6)	3	44–52(48.7)	—	—	—	—
Height of 2nd dorsal fin										
Atlantic	2	22(22.0)	16	19–24(21.8)	6	17–23(20.7)	1	22	1	23
Eastern Pacific	—	—	8	18–23(21.0)	4	18–22(20.8)	—	—	—	—
Western Pacific and Indo-Australia	2	21–23(22.0)	12	16–22(20.2)	3	20–21(20.3)	—	—	1	23
Length of anal base										
Atlantic	2	53–56(54.5)	16	48–60(53.8)	6	47–55(51.5)	1	47	1	53
Eastern Pacific	—	—	8	48–59(51.9)	4	45–51(49.0)	—	—	—	—
Western Pacific and Indo-Australia	2	51–54(52.5)	12	43–54(50.2)	3	48–64(54.7)	—	—	1	40
Length of anal lobe										
Atlantic	2	40(40.0)	16	33–46(38.9)	6	37–45(40.3)	1	40	1	40
Eastern Pacific	—	—	8	35–43(38.9)	4	37–41(38.8)	—	—	—	—
Western Pacific and Indo-Australia	2	38–47(42.5)	12	34–44(40.2)	3	38–39(38.3)	—	—	—	—
Height of anal fin										
Atlantic	2	28–30(29.0)	16	28–34(30.5)	6	27–33(29.2)	1	28	1	29
Eastern Pacific	—	—	8	26–31(28.9)	4	27–34(29.8)	—	—	—	—
Western Pacific and Indo-Australia	2	26–29(27.5)	12	24–32(28.3)	3	29–32(30.0)	—	—	1	25
Length of pectoral base										
Atlantic	2	59–61(60.0)	16	50–61(54.6)	6	48–60(53.0)	1	51	1	50
Eastern Pacific	—	—	8	48–57(52.1)	4	49–55(53.0)	—	—	—	—
Western Pacific and Indo-Australia	2	61(61.0)	12	48–57(51.8)	3	51–59(55.0)	—	—	—	—
Length of pelvic base										
Atlantic	2	53–54(53.5)	16	49–59(54.2)	6	49–54(51.5)	1	50	1	50
Eastern Pacific	—	—	8	49–58(53.9)	4	47–54(51.5)	—	—	—	—
Western Pacific and Indo-Australia	2	51–54(52.5)	12	50–60(53.9)	3	48–55(52.0)	—	—	—	—
Length of caudal fin										
Atlantic	2	305–314(309.5)	16	291–332(316.4)	6	287–318(302.7)	1	295	1	284
Eastern Pacific		—	8	300–325(313.9)	4	294–327(308.0)		—		—
Western Pacific and Indo-Australia	2	308–317(312.5)	12	296–323(313.3)	3	295–308(302.0)		—		—

TABLE 6.—*Measurements of subspecies of* Sphyrna tiburo (*proportions expressed in thousandths of total length*)

	Size range in mm. (N=number of specimens, A=Atlantic, P=Pacific)							
	N	200–399	N	400–599	N	600–799	N	>800
Head width	8							
tiburo (A)	3	186–229(206.0)	14	178–204(188.6)	12	160–192(174.1)	7	143–189(168.0)
vespertina (P)		215–245(227.7)	8	194–213(202.4)	5	185–203(193.0)	4	175–188(180.3)
Internarial distance								
tiburo (A)	8	137–156(144.9)	14	121–148(131.7)	12	114–129(119.7)	7	100–132(118.4)
vespertina (P)	3	153–160(156.0)	8	140–155(146.1)	5	125–144(133.2)	4	122–140(130.8)
Snout to symphysis								
tiburo (A)	8	94–99(97.0)	14	78–90(83.9)	12	72–80(76.0)	7	73–82(75.8)
vespertina (P)	3	93–96(94.5)	8	82–91(86.0)	5	75–82(79.0)	4	73–81(77.0)

TABLE 6.—*Measurements of subspecies of* Sphyrna tiburo (*proportions expressed in thousandths of total length*)—Continued

	Size range in mm. (N=number of specimens, A=Atlantic, P=Pacific)							
	N	200–399	N	400–599	N	600–799	N	>800
Head length								
tiburo (A)	8	234–249(242.8)	14	216–244(228.7)	12	205–223(214.9)	7	201–227(212.3)
vespertina (P)	3	238–246(242.0)	8	222–240(231.9)	5	208–215(214.3)	4	200–215(208.8)
Snout to 1st gill slit								
tiburo (A)	8	186–204(195.4)	14	173–196(183.3)	12	159–185(170.8)	7	153–174(163.7)
vespertina (P)	3	190–196(193.3)	8	178–194(187.8)	5	162–180(173.0)	4	157–169(162.5)
Snout to 1st dorsal origin								
tiburo (A)	8	295–331(309.9)	14	287–326(303.9)	12	268–319(295.4)	7	277–310(298.6)
vespertina (P)	3	297–316(307.7)	8	283–312(298.9)	5	279–333(302.3)	4	280–300(290.8)
Snout to 2nd dorsal origin								
tiburo (A)	8	576–611(591.8)	14	588–625(601.5)	12	595–634(610.3)	7	605–634(614.2)
vespertina (P)	3	587–600(594.3)	8	556–619(598.1)	5	585–628(608.6)	4	600–636(615.0)
Distance between 1st and 2d dorsal bases								
tiburo (A)	8	181–202(188.4)	14	192–219(207.1)	12	199–233(218.7)	7	214–253(235.0)
vespertina (P)	3	188–191(189.7)	8	189–212(202.6)	5	204–229(212.8)	4	214–242(230.3)
Snout to pectoral insertion								
tiburo (A)	8	220–243(233.3)	14	203–230(213.8)	12	188–222(201.3)	7	194–214(203.8)
vespertina (P)	3	224–240(231.0)	8	200–235(218.2)	5	195–215(205.1)	4	185–220(197.3)
Snout to pelvic insertion								
tiburo (A)	8	421–446(431.3)	14	430–450(438.2)	12	426–456(444.0)	7	385–471(442.3)
vespertina (P)	3	427–448(436.7)	8	428–470(445.3)	5	412–446(427.4)	4	435–455(443.8)
Horizontal diameter of orbit								
tiburo (A)	8	21–23(22.3)	14	19–23(20.1)	12	18–20(18.8)	7	15–17(16.0)
vespertina (P)	3	21–24(22.3)	8	18–23(20.4)	5	16–20(18.2)	4	14–18(16.3)
Length of 1st dorsal base								
tiburo (A)	8	85–97(90.1)	14	90–106(96.1)	12	93–110(100.4)	7	92–107(98.7)
vespertina (P)	3	88–98(92.0)	8	77–102(93.3)	5	86–101(92.4)	4	98–104(100.3)
Length of 2nd dorsal base								
tiburo (A)	8	46–52(48.8)	14	42–58(50.8)	12	44–57(50.8)	7	41–57(47.8)
vespertina (P)	3	47–51(49.0)	8	42–55(48.2)	5	42–52(47.2)	4	45–51(48.0)
Length of 2nd dorsal lobe								
tiburo (A)	8	38–49(44.1)	14	39–51(46.6)	12	43–53(48.6)	7	45–55(50.0)
vespertina (P)	3	43–47(45.0)	8	43–51(47.0)	5	47–53(49.8)	4	48–56(52.7)
Height of 2nd dorsal fin								
tiburo (A)	8	24–41(33.5)	14	31–41(35.8)	12	35–43(39.3)	7	35–41(37.5)
vespertina (P)	3	26–37(32.0)	8	32–40(35.4)	5	34–43(38.2)	4	38–44(40.3)
Length of anal base								
tiburo (A)	8	70–84(75.5)	14	65–86(73.4)	12	64–89(76.3)	7	71–83(79.8)
vespertina (P)	3	74–83(78.3)	8	69–88(77.6)	5	69–88(79.0)	4	73–85(76.8)
Length of anal lobe								
tiburo (A)	8	33–39(35.5)	14	32–39(33.6)	12	27–38(34.8)	7	25–37(32.8)
vespertina (P)	3	31–38(34.7)	8	35–39(37.3)	5	33–39(36.4)	4	30–37(34.3)
Height of anal fin								
tiburo (A)	8	36–38(34.0)	14	28–35(32.3)	12	30–38(33.0)	7	30–36(32.0)
vespertina (P)	3	35–38(36.3)	8	29–37(33.4)	5	33–38(35.0)	4	26–36(32.3)
Length of pectoral base								
tiburo (A)	8	49–63(56.3)	14	53–65(59.6)	12	51–69(59.3)	7	57–66(60.3)
vespertina (P)	3	58–60(59.3)	8	56–64(60.4)	5	54–60(56.3)	4	58–67(62.5)
Length of pelvic base								
tiburo (A)	8	52–63(57.5)	14	55–64(59.4)	12	58–67(62.3)	7	60–66(62.3)
vespertina (P)	3	52–60(55.7)	8	56–70(61.0)	5	55–65(58.8)	4	58–64(61.5)
Length of caudal fin								
tiburo (A)	8	281–307(292.0)	14	266–294(280.9)	12	250–291(270.1)	7	234–276(258.9)
vespertina (P)	3	288–295(292.3)	8	278–294(287.5)	5	269–296(280.6)	4	249–270(255.8)

TABLE 7.—*Measurements of* Sphyrna media (*proportions expressed in thousandths of total length*)

	Size range in mm.			
	200–399	400–599	600–799	>800
	Number of specimens			
	7	3	2	2
Head width	231–333(289.3)	223–264(247.3)	232–236(234.0)	228–232(230.0)
Internarial distance	182–204(194.0)	162–191(177.0)	166–171(168.5)	167–169(168.0)
Snout to symphysis	100–107(103.7)	88–97(91.3)	80–84(82.0)	76–81(78.5)
Mouth width	67–76(71.7)	61–71(65.7)	62–65(63.5)	62–72(67.0)
Head length	251–264(256.7)	222–257(242.7)	218	211–238(224.5)
Snout to 1st gill slit	204–216(210.7)	183–200(192.7)	171–179(175.0)	176–215(195.5)
Snout to 1st dorsal origin	301–321(306.7)	267–322(302.0)	285–300(292.5)	281–306(293.5)
Snout to 2nd dorsal origin	592–619(605.5)	575–628(604.7)	598–618(608.0)	615–645(630.0)
Distance between 1st and 2nd dorsal bases	182–196(192.0)	202–216(207.0)	213	227–233(230.0)
Snout to pectoral insertion	231–251(245.3)	206–241(222.3)	211–226(218.5)	195–210(202.5)
Snout to pelvic insertion	421–439(432.0)	418–446(429.3)	421–437(429.0)	387–392(389.5)
Horizontal diameter of orbit	19–25(20.9)	18–21(19.3)	16–17(16.5)	14–15(14.5)
Length of 1st dorsal base	97–111(103.8)	90–99(93.7)	90–105(97.5)	106–107(106.5)
Length of 2nd dorsal base	43–52(48.0)	44–46(45.0)	45–50(47.5)	44–49(46.5)
Length of 2nd dorsal lobe	45–49(47.1)	48–51(49.7)	51–54(102.5)	55–63(59.0)
Height of 2nd dorsal fin	30–38(34.3)	30–37(33.0)	35–39(37.0)	39
Length of anal base	72–83(80.3)	73–84(80.0)	86–90(88.0)	84–85(84.5)
Length of anal lobe	36–38(37.3)	39	31–38(34.5)	39–48(43.5)
Height of anal fin	39–47(42.5)	38–43(40.7)	39–46(42.5)	41
Length of pectoral base	50–57(53.8)	53–57(54.3)	52–56(54.0)	59–62(60.5)
Length of pelvic base	54–62(59.2)	60–65(62.3)	48–61(54.5)	66–67(66.5)
Length of caudal fin	279–297(289.3)	290–310(298.0)	287–297(292.0)	289–306(297.5)

TABLE 8.—*Measurements of* Sphyrna corona (*proportions expressed in thousandths of total length*)

	Size range in mm.		
	200–399	400–599	>600
	Number of specimens		
	12	2	1
Head width	259–291(275.4)	261–262(261.5)	237
Internarial distance	181–206(192.3)	203–210(182.0)	161
Snout to symphysis	110–127(117.1)	107–109(108.0)	88
Mouth width	59–69(65.6)	60–63(61.5)	57
Head length	250–281(270.3)	251–261(256.0)	223
Snout to 1st gill slit	209–230(218.9)	203–210(206.5)	179
Snout to 1st dorsal origin	315–345(328.6)	309–318(313.5)	312
Snout to 2nd dorsal origin	595–640(613.9)	588–617(602.5)	625
Distance between 1st and 2nd dorsal bases	174–202(188.1)	185–205(195.0)	228
Snout to pectoral insertion	253–277(262.3)	238–263(250.5)	236
Snout to pelvic insertion	436–465(450.1)	428–447(437.5)	438
Horizontal diameter of orbit	17–22(18.8)	17–18(17.5)	13
Length of 1st dorsal base	89–104(97.4)	94	85
Length of 2nd dorsal base	39–47(43.6)	43–49(46.0)	39
Length of 2nd dorsal lobe	40–52(45.1)	46–49(47.5)	48
Height of 2nd dorsal fin	28–33(30.4)	30–34(32.0)	33
Length of anal base	82–92(87.5)	87–89(88.0)	86
Length of anal lobe	33–43(37.8)	40–41(40.5)	36
Height of anal fin	32–41(36.8)	40–43(41.5)	36
Length of pectoral base	52–61(55.6)	55–59(57.0)	50
Length of pelvic base	48–60(53.1)	53–59(56.0)	61
Length of caudal fin	268–290(279.3)	284–288(286.0)	265

TABLE 9.—*Measurements of* Sphyrna tudes (*proportions expressed in thousandths of total length*)

	Size range in mm. (N=number of specimens)							
	N	200–399	N	400–599	N	600–799	N	>800
Head width								
Western Atlantic	13	299–319(310.0)	1	304	2	276–285(280.5)	1	280
Mediterranean	1	321	0	—	0	—	0	—
Internarial distance								
Western Atlantic	13	221–234(228.5)	1	219	2	202–209(205.5)	1	206
Mediterranean	1	231	0	—	0	—	0	—
Snout to symphysis								
Western Atlantic	13	94–117(105.1)	1	92	2	80(80.0)	1	72
Mediterranean	1	104	0	—	0	—	0	—
Mouth width								
Western Atlantic	13	61–69(64.7)	1	68	2	65–69(67.0)	1	69
Mediterranean	1	69	0	—	0	—	0	—
Head length								
Western Atlantic	13	229–263(242.2)	1	233	2	224–226(225.0)	1	227
Mediterranean	1	243	0	—	0	—	0	—
Snout to 1st gill slit								
Western Atlantic	13	190–211(200.5)	1	193	2	186–189(187.5)	1	184
Mediterranean	1	197	0	—	0	—	0	—
Snout to 1st dorsal origin								
Western Atlantic	13	293–334(309.8)	1	305	2	299–306(302.5)	1	290
Mediterranean	1	319	0	—	0	—	0	—
Snout to 2nd dorsal origin								
Western Atlantic	13	580–625(597.0)	1	606	2	601–619(610.0)	1	622
Mediterranean	1	243	0	—	0	—	0	—
Distance between 1st and 2nd dorsal bases								
Western Atlantic	13	178–209(190.7)	1	203	2	199–209(204.0)	1	224
Mediterranean	1	182	0	—	0	—	0	—
Snout to pectoral insertion								
Western Atlantic	13	215–251(231.1)	1	225	2	227–228(227.5)	1	212
Mediterranean	1	246	0	—	0	—	0	—
Snout to pelvic insertion								
Western Atlantic	13	397–427(413.5)	1	412	2	405–428(416.5)	1	393
Mediterranean	1	434	0	—	0	—	0	—
Horizontal diameter of orbit								
Western Atlantic	13	15–23(18.0)	1	15	2	15(15.0)	1	18
Mediterranean	1	20	0	—	0	—	0	—
Length of 1st dorsal base								
Western Atlantic	13	89–109(98.0)	1	108	2	103–104(103.5)	1	108
Mediterranean	1	95	0	—	0	—	0	—
Length of 2nd dorsal base								
Western Atlantic	13	41–51(44.2)	1	45	2	41–44(42.5)	1	48
Mediterranean	1	45	0	—	0	—	0	—
Length of 2nd dorsal lobe								
Western Atlantic	13	41–47(44.0)	1	47	2	53–58(55.5)	1	56
Mediterranean	1	42	0	—	0	—	0	—
Height of 2nd dorsal fin								
Western Atlantic	13	29–33(31.0)	1	29	2	33–36(34.5)	1	39
Mediterranean	1	35	0	—	0	—	0	—
Length of anal base								
Western Atlantic	13	75–99(84.6)	1	83	2	83–93(88.0)	1	84
Mediterranean	1	84	0	—	0	—	0	—
Length of anal lobe								
Western Atlantic	13	28–33(32.1)	1	37	2	37–42(39.5)	1	34
Mediterranean	1	35	0	—	0	—	0	—
Height of anal fin								
Western Atlantic	13	36–47(40.4)	1	46	2	47(47.0)	1	47
Mediterranean	1	51	0	—	0	—	0	—

TABLE 9.—*Measurements of* Sphyrna tudes (*proportions expressed in thousandths of total length*)—Continued

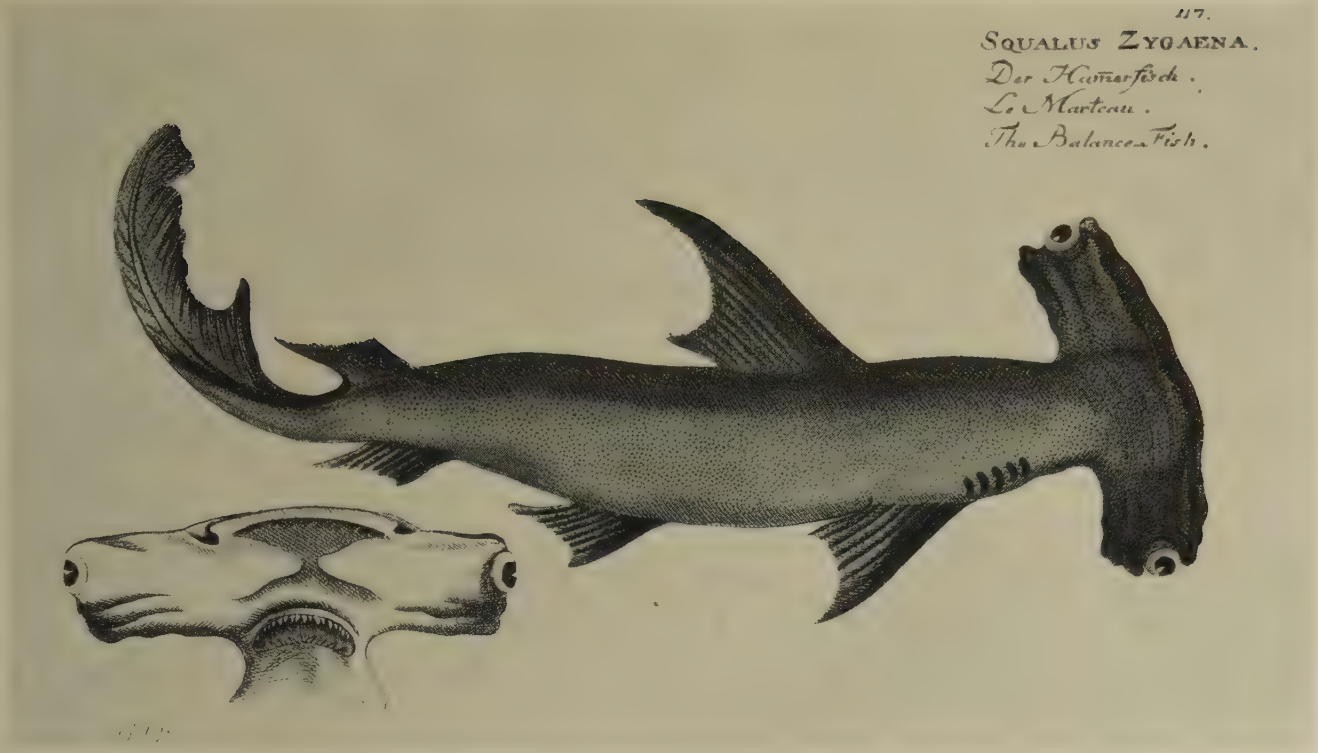
	Size range in mm. (N=number of specimens)							
	N	200–399	N	400–599	N	600–799	N	>800
Length of pectoral base								
Western Atlantic	13	53–58(55.2)	1	57	2	60–62(61.0)	1	59
Mediterranean	1	55	0	—	0	—	0	—
Length of pelvic base								
Western Atlantic	13	50–60(55.0)	1	54	2	64–67(65.5)	1	73
Mediterranean	1	59	0	—	0	—	0	—
Length of caudal fin								
Western Atlantic	13	290–313(302.4)	1	295	2	293–297(295.0)	1	286
Mediterranean	1	292	0	—	0	—	0	—

TABLE 10.—*Measurements of heads of* Sphyrna lewini *and* S. couardi *from Gulf of Guinea* [1]

	Head width	Snout to symphysis	Nares to posterior margin of head [2]	Mouth gape	Inner narial groove
S. lewini	445.0	93.5	93.5	103.5	83.0
proportion	—	.210	.210	.233	.187
S. couardi	425.0	115.0	117.5	119.5	89.0
proportion	—	.270	.276	.281	.209

[1] One specimen from each species. Under each species the first row represents the empirical lengths (in millimeters); the second row, the proportional values (in thousandths of head width), obtained by dividing head width into the respective measurements.

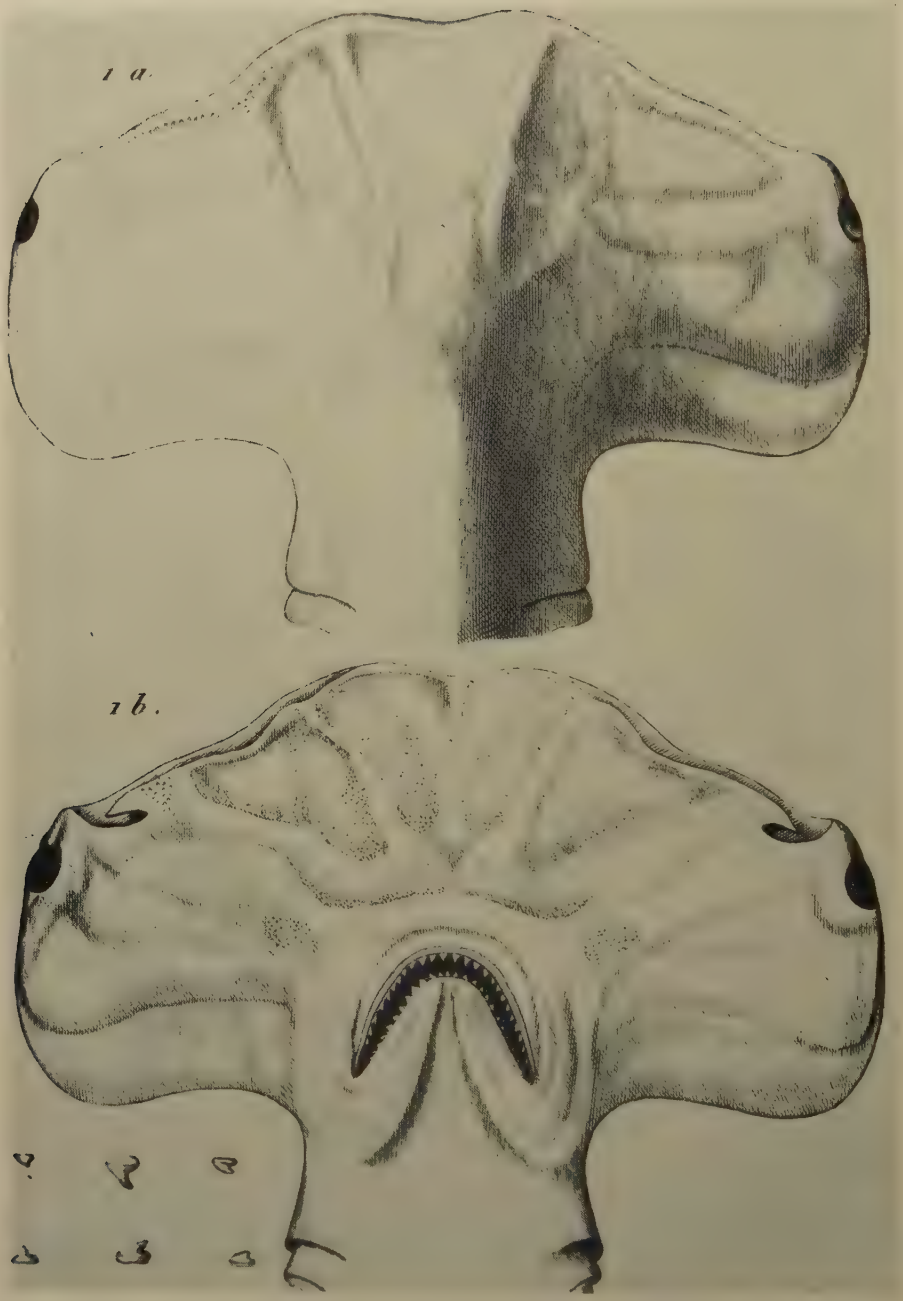
[2] Shortest vertical distance.



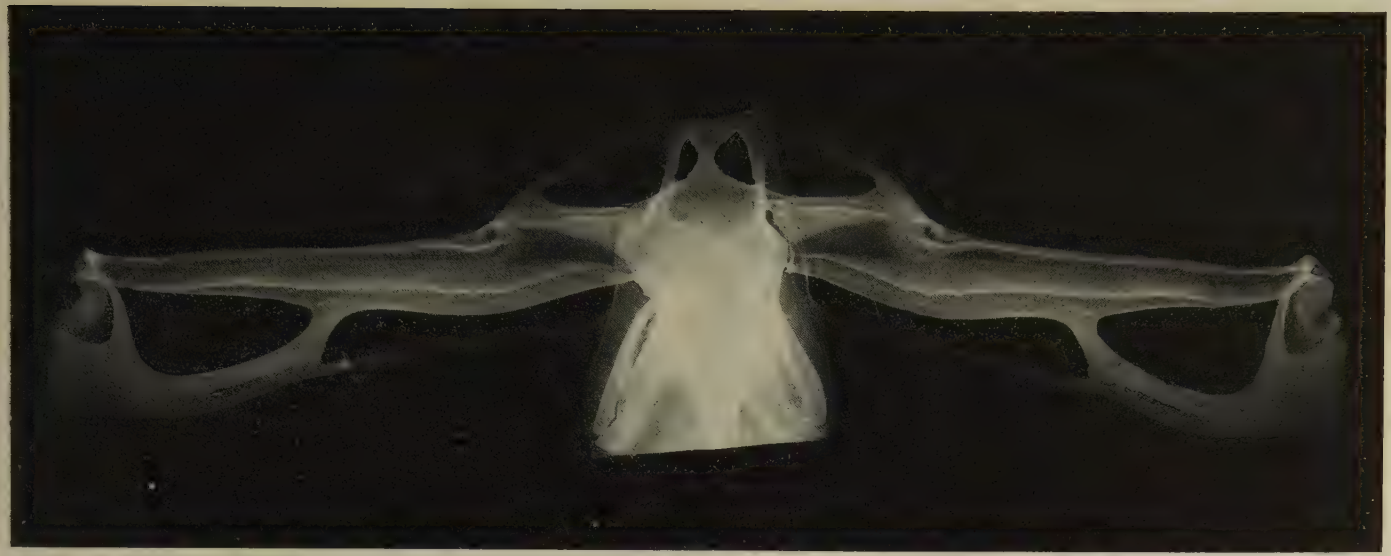
Original illustration of *Zygaena blochii* (misidentified as *Squalus zygaena*), from Bloch (1785, vol. 1, pl. 117).

Original illustration of *Zygaena mokarran*, from Rüppell (1835, pl. 17, fig. 3).

Original illustration of *Zygaena lewini*, from Griffith and Smith, *in* Cuvier, Griffith, and Smith (1834, p. 640, pl. 50).

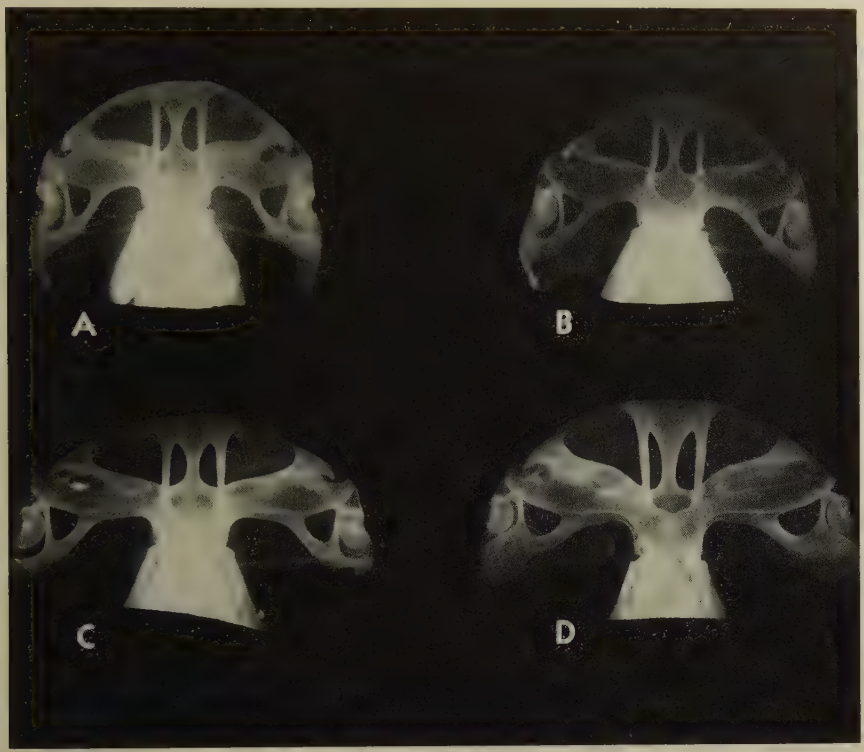


Original illustration of *Zygaena tudes*, from Valenciennes (1822, pl. 12, figs. 1a, b).



Radiograph of chondrocranium of *Sphyrna blochii*, a specimen 470 mm. TL, from Java (FMNH 15656).

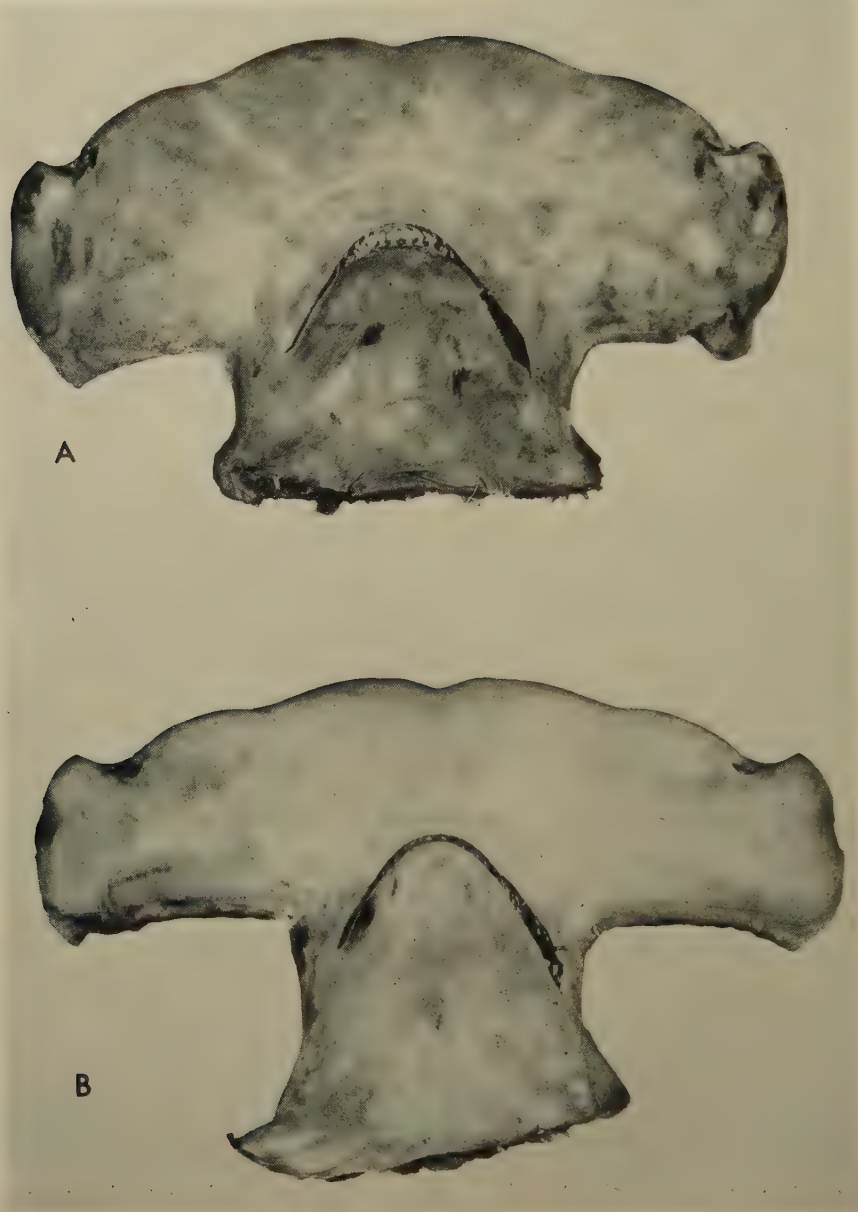
Radiographs of chondrocrania of several species of *Sphyrna:* A, *S. mokarran*, 560 mm. TL, from Florida (USNM 186087); B, *S. lewini*, 447 mm. TL, from Liberia (USNM 179706); C, *S. zygaena*, 590 mm. TL, from Italy (USNM 28452).



Radiographs of chondrocrania of several species of *Sphyrna:* A, *S. tiburo tiburo,* 388 mm. TL, from Nicaragua (USNM 78180; B, *S. tiburo vespertina,* 545 mm. TL, from Mexico (UCLA 51–4); C, *S. media,* 337 mm. TL, from Mexico (FMNH 63093); D, *S. corona,* 371 mm. TL, from Mexico (FMNH 72521, ex. 63093).

Radiographs of chondrocrania of *Sphyrna tudes:* A, a specimen 390 mm. TL (holotype of *S. bigelowi*) from Uruguay (USNM 87682); B, a specimen 346 mm. TL (lectotype of *S. tudes*) from France (MNHN 1049).

Radiographs of chondrocrania: A, *S. couardi*, head 425 mm. wide, from Guinea (USNM uncat.); B, *S. lewini*, head 445 mm. wide, from Guinea (USNM uncat.).



Photographs of heads: A, *S. couardi*, head 425 mm. wide, from Guinea (USNM uncat.); B *S. lewini*, head 445 mm. wide, from Guinea (USNM uncat.).